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Disintegration of the genus *Prosopis* L. (Leguminosae, Caesalpinioideae, mimosoid clade)

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Abstract

Robust evidence from phylogenomic analyses of 997 nuclear genes has recently shown, beyond doubt, that the genus *Prosopis* is polyphyletic with three separate lineages, each with affinities to other genera of mimosoids: (i) *Prosopis africana* is an isolated lineage placed in the grade of *Plathymenia*, *Newtonia* and *Fillaeopsis* that subtends the core mimosoid clade; (ii) the remaining Old World species of *Prosopis* form a clade that is sister to the Indo-Nepalese monospecific genus *Indopiptadenia* and (iii) New World *Prosopis* has the Namibian / Namaqualand monospecific endemic genus *Xerocladia* nested within it. This means that it is now clear that maintaining the unity of the genus *Prosopis* sensu Burkart (1976) is no longer tenable. These three distinct lineages of *Prosopis* species correspond directly to Burkart's (1976) sectional classification of the genus, to previously recognised genera and to the differences in types of armature that underpin Burkart's sections. Here, we address this non-monophyly by resurrecting three segregate genera – *Anonychium*, *Neltuma* and *Strombocarpa* and provide 57 new name combinations where necessary, while maintaining the morphologically distinctive and geographically isolated genera *Xerocladia* and *Indopiptadenia*. The genus *Prosopis* itself is reduced to just three species and an emended description is presented. The impacts of these name changes for a genus of such high ecological and human use importance are discussed. These impacts are mitigated by clear differences in armature which facilitate identification and by potential benefits from the deeper biological understanding brought about

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by recognition of these divergent lineages at generic rank. We provide an identification key to genera and present a map showing the distributions of the segregate genera, as well as drawings and photos illustrating variation in armature and fruits.

Keywords

Anonychium, Fabaceae, generic delimitation, *Indopiptadenia*, monophyly, *Neltuma*, *Strombocarpa*, taxonomy, *Xerocladia*

Introduction

Burkart's (1976) worldwide taxonomic monograph of the genus *Prosopis* L. recognised 44 species placed in five sections. Since then, 13 additional species have been described (Schinini 1981; Earl and Lux 1991; Palacios 2006; Vásquez Núñez et al. 2009; De Mera et al. 2019) one of which, *P. bonplanda* P.R. Earl & Lux, was subsequently treated as a synonym by Palacios (2006). All of these additional species belong morphologically in section *Algarobia* DC., such that the generic unity and infrageneric classification, proposed by Burkart (1976), remain the current framework for understanding the genus. Following Bentham (1875), Burkart (1976) justified the generic unity of a widely delimited *Prosopis*, based on the broad uniformity of flowers and fruits across *Prosopis* s.l. Perhaps the most important uniting feature was the modified indehiscent cylindrical or thickened legume, with a more or less sugary, fleshy or fibrous mesocarp and an endocarp more or less hardened and segmented into one-seeded coriaceous to bony seed chambers, these closed or sometimes opening easily. Fruits of this type are eagerly consumed by herbivores, including all kinds of livestock, the seeds benefiting from scarification as they pass through the digestive tract and as a result being widely dispersed (see below), a seed dispersal syndrome that unites all species of *Prosopis* s.l. Moreover, Burkart (1976) explicitly downplayed vegetative characters and notably variation in armature, as of less significance for classification, stating that "the main differences between sections *Prosopis*, *Algarobia* and *Strombocarpa* Benth. are vegetative spine characters and are, therefore, only of subgeneric rank" (Burkart 1976: 227), even though he acknowledged that the variation in armature probably had phylogenetic significance (see below).

This long-held generic concept of *Prosopis* established by Bentham (1842, 1875) and followed by Burkart in his 1976 monograph, is no longer sustainable, because molecular phylogenies have demonstrated, beyond doubt, that *Prosopis* is polyphyletic. This non-monophyly was first revealed by Catalano et al. (2008) and confirmed by LPWG (2017) who showed that *P. africana* (Guill. & Perr.) Taub. forms an isolated monospecific lineage quite separate from the rest of *Prosopis* and that the monospecific Namibian/S. African endemic genus *Xerocladia* Harv. was potentially nested within *Prosopis*, but these analyses lacked robust support and sampling of critical taxa. Recent phylogenomic analyses of a much larger DNA sequence dataset, based on 997 nuclear genes (Koenen et al. 2020) that now includes all but five of the 152 genera of

Caesalpinioideae (Ringelberg et al. 2022), have confirmed this non-monophyly showing robust support for three separate lineages (Fig. 1): (i) a lineage comprising *P. africana*, which is placed in a grade made up of the genera *Plathymenia* Benth., *Fillaeopsis* Harms and *Newtonia* Baill., as found by Catalano et al. (2008); (ii) a lineage comprising the remaining Old World species of *Prosopis* which is robustly supported as sister to the monospecific genus *Indopiptadenia* Brenan from the Himalayan foothills of the Terai border region of Nepal and India (Bajpai et al. 2014); (iii) a lineage comprising the New World species of *Prosopis* plus the Namibian/South African endemic genus *Xerocladia*, which is nested within this clade, again confirming the preliminary results of Catalano et al. (2008). The DNA sequence dataset of Ringelberg et al. (2022), based as it is on a large number of nuclear genes, can also be used to quantify how many genes support a particular species tree topology and, thereby, how robust the phylogeny is (Fig. 1B) and also how many genes support alternative species tree topologies. These analyses show that just 69 gene trees support a sister group relationship between sections *Strombocarpa* (= *Strombocarpa*) and *Algarobia* + *Monilicarpa* Ruiz Leal & Burkart (= *Neltuma* Raf.), while 629 of the gene trees conflict with that topology (Fig. 1C) and none of the gene trees supports a monophyletic *Prosopis* s.l. (Fig. 1D), confirming that there is an overwhelming number of gene trees supporting the species tree topology in Fig. 1B. It is thus now clear that maintaining *Prosopis* in its current circumscription is untenable.

What is immediately striking from Fig. 1 and the earlier phylogeny of Catalano et al. (2008) with its denser sampling of species across New World *Prosopis*, is that these three separate lineages of *Prosopis* species correspond to and are congruent with Burkart's sections (apart from the inclusion of *Xerocladia*) and with the variation in armature upon which Burkart's sections were based (Figs 2–4): Section *Anonychium* Benth. = *P. africana*, is unarmed in common with the rest of the grade of lineages (*Plathymenia*, *Fillaeopsis* and *Newtonia*) that subtend the large core mimosoid clade of Koenen et al. (2020) (Fig. 1; Ringelberg et al. 2022); Section *Prosopis* = the rest of Old World *Prosopis*, comprising *P. cineraria* (L.) Druce, *P. farcta* (Banks & Sol.) J.F. Macbr. and *P. koelziana* Burkart (from Iran), all have straight internodal prickles (Figs 2C, M and 3C), which are also found in the sister genus of this clade, *Indopiptadenia*, including in the form of large, conical, hard, sharp-pointed spines on older stems and trunk (Fig. 3B; see also Bajpai et al. 2014: figs 2B–H and 11A); species of Section *Strombocarpa* plus the genus *Xerocladia* have stipular spines (Figs 2E, H, I, O and 3A, D); and species of sections *Monilicarpa* + *Algarobia* variously have spinescent shoots or uninodal axillary solitary or geminate spines (Figs 2A, B, D, F, G, J–L, N and 3E, F and 4), but never the internodal prickles of section *Prosopis*, nor the stipular spines of section *Strombocarpa* (see also Benson 1941). These three types of armature are non-homologous, even though they have evolved to meet similar plant defence functions and can look superficially similar. To explore the evolution of armature across the *Prosopis* s.l. grade, we scored these different types of armature across genera of subfamily Caesalpinioideae and optimised these on to the Ringelberg et al. (2022) phylogeny. This reconstruction shows independent derivations of stipular spines, internodal prickles and axillary nodal spines (Fig. 4), each providing diagnostic synapomorphies for

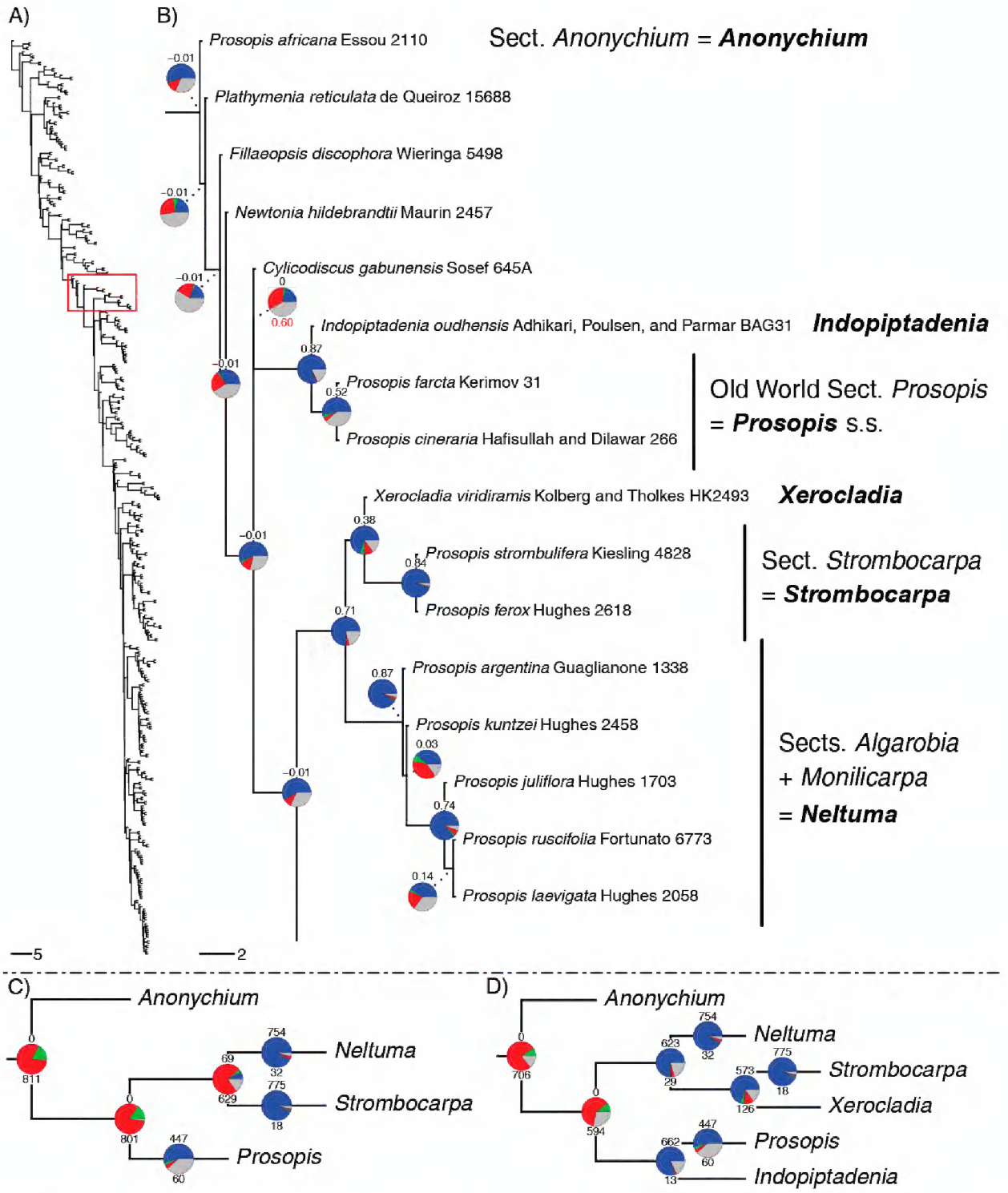

Figure 1. A Phylogeny of the Caesalpinioideae showing the placement of the *Prosopis* grade (boxed in red) within the subfamily, based on analyses of DNA sequences of 997 nuclear genes (Ringelberg et al. 2022) **B** the part of the phylogeny that includes all elements of *Prosopis* s.l. Genera recognised in the new generic system presented here are in **bold**. Pie charts show the fraction of gene trees supporting that bipartition in blue, the fraction of gene trees supporting the most likely alternative configuration in green, the fraction of gene trees supporting additional conflicting configurations in red and the fraction of uninformative gene trees in grey. Numbers above pie charts are Extended Quadripartition Internode Certainty (Zhou et al. 2020) scores. Branch lengths are expressed in coalescent units and terminal branches were assigned an arbitrary uniform length for visual clarity, see Ringelberg et al. (2022); the root is not drawn to scale **C, D** the two most likely alternative tree topologies which would allow for a monophyletic *Prosopis* s.l., either without (**C**) or with (**D**) *Xerocladia* and *Indopiptadenia*. In **C** and **D** numbers above pie charts = number of gene trees supporting the species tree, numbers below pie charts = number of gene trees conflicting with the species tree **C** lack of gene tree support (just 69 gene trees) for the alternative species tree topology where sections *Algarobia* + *Monilicarpa* (≡ *Neltuma*) are sister to section *Strombocarpa* (≡ *Strombocarpa*) vs. 573 genes supporting a sister group relationship between *Strombocarpa* and *Xerocladia* (as shown in **D**) **D** lack of gene trees (zero gene trees) supporting a monophyletic *Prosopis* s.l.

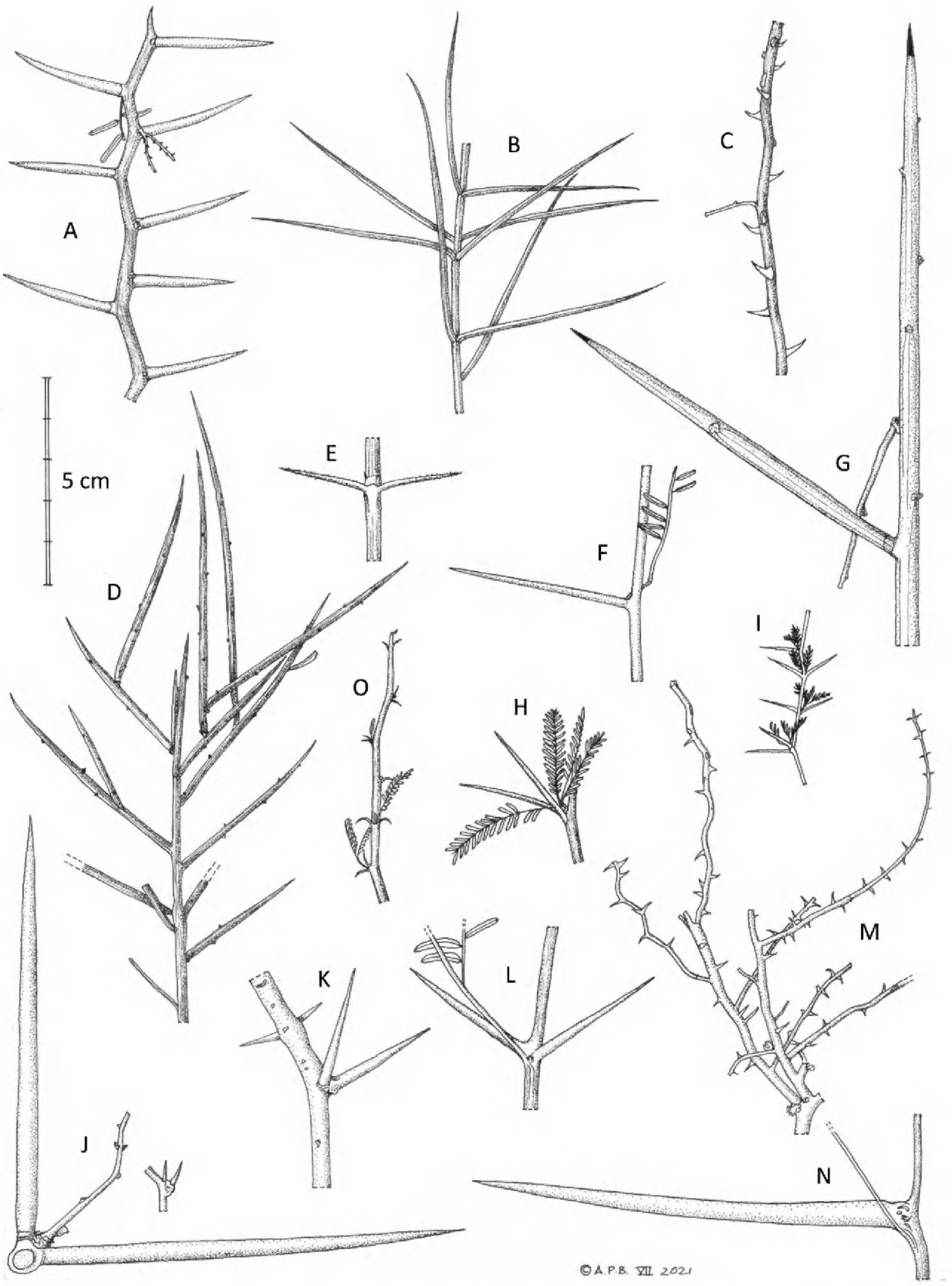

Figure 2. Variation in armature of *Prosopis*, *Strombocarpa*, *Neltuma* and *Xerocladia* **A** *Neltuma denudans* (nodal spines on a zig-zag stem) **B** *N. humilis* (paired striate spine-tipped branches) **C** *Prosopis cineraria* (scattered internodal prickles) **D** *Neltuma sericantha* (spine-tipped stems) **E** *Strombocarpa burkartii* (stipular spines) **F** *Neltuma argentina* (single nodal axillary spine) **G** *N. kuntzei* (spinescent shoots) **H** *Strombocarpa ferox* (stipular spines) **I** *S. strombulifera* (stipular spines) **J** *Neltuma elata* (variation in paired nodal spines on one specimen) **K** *N. alba* (paired nodal spines) **L** *N. velutina* (paired nodal spines) **M** *Prosopis farcta* (scattered internodal prickles) **N** *Neltuma ruscifolia* (single nodal axillary spine) **O** *Xerocladia viridiramis* (recurved, deflexed stipular spines) (5 cm scale bar). All specimens at K **A** drawn from *Seijo* 1489 **B** *Tweedie* s.n. **C** *Willcox* 299 **D** MERL 8792 **E** *Acosta & Rosas* 748 **F** *Guaglianone et al.* 1762 **G** *Nee & Coimbra* 35556 **H** *Atahuachi* et al. MA1147 **I** *Hunziker* 2036 **J** *Legname & Cuezzo* 10396 (large and small spines from same specimen) **K** *Hughes & Forrest* 2312 **L** *Harding & Balsinhas* 140 **M** *Guest et al.* 17463 **N** *Wood & Mamani* 14063 **O** *Kolberg & Tholkes* HK2493. Drawn by Andrew Brown, July 2021.

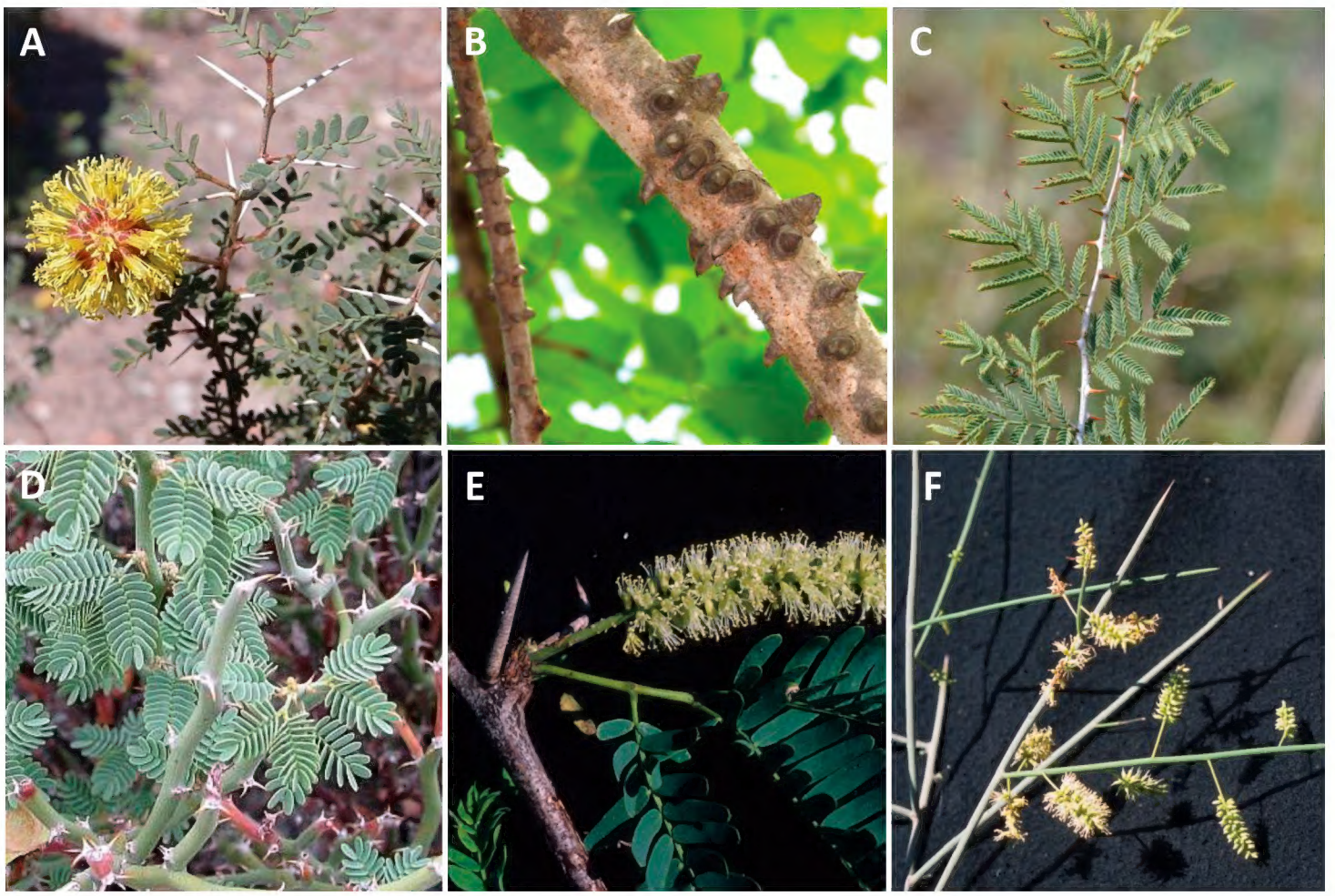

Figure 3. Variation in armature across *Prosopis* s.l. and allies **A** stipular spines of *Strombocarpa strombulifera* **B** internodal prickles on shoots and branches of *Indopiptadenia oudhensis* which it shares with its sister group, *Prosopis* s.s. illustrated in **C**; **C** internodal prickles of *Prosopis farcta* **D** stipular spines of *Xerocladia viridiramis* which it shares with its sister group, the genus *Strombocarpa* illustrated in **A**; **E** axillary nodal spines of *Neltuma juliflora* **F** spinescent straight cylindrical shoots of the subaphyllous *Neltuma kuntzei*. Photos courtesy of Guillermo Debandi (**A**) (see https//www.inaturalist.org/taxa/78750-Prosopis-strombulifera/browse_photos), Dr. Omesh Bajpai and Dr. Lal Babu Chaudhary (**B**), Zeynel Cebeci (**C**) (see https//commons.wikimedia.org/wiki/FileProsopis_farcta_-_Syrian_mesquite_01), N. Dreber (**D**) (see http//www.southernafricanplants.com/), Colin Hughes (**E, F**).

clades in the context of *Prosopis* s.l. (Fig. 4). Ironically, in his justification of the unity of *Prosopis*, Burkart (1976) pointed to *Acacia* Mill. s.l. as another group that also showed considerable diversity in types of armature and other vegetative traits, but which was considered (at that time) to comprise a single genus. Given that *Acacia* s.l. was later demonstrated to be polyphyletic (reviewed by Maslin et al. 2003) and has now been dismantled into seven segregate genera, several of which are distinguished primarily by differences in armature (e.g. the stipular spines that distinguish *Vachellia* Wight & Arn. from the cauline nodal and internodal prickles of *Senegalia* Raf.), Burkart's suggestion that a wide concept of *Acacia* chimed with his wide concept of *Prosopis* can now be seen with hindsight to have been misplaced.

The apparent phylogenetic significance of types of armature to distinguish important clades and genera across Caesalpinioideae, contrasts with the striking evolutionary lability of fruit types, as seen across *Prosopis* s.l. and allies (Figs 5–7). This is exemplified

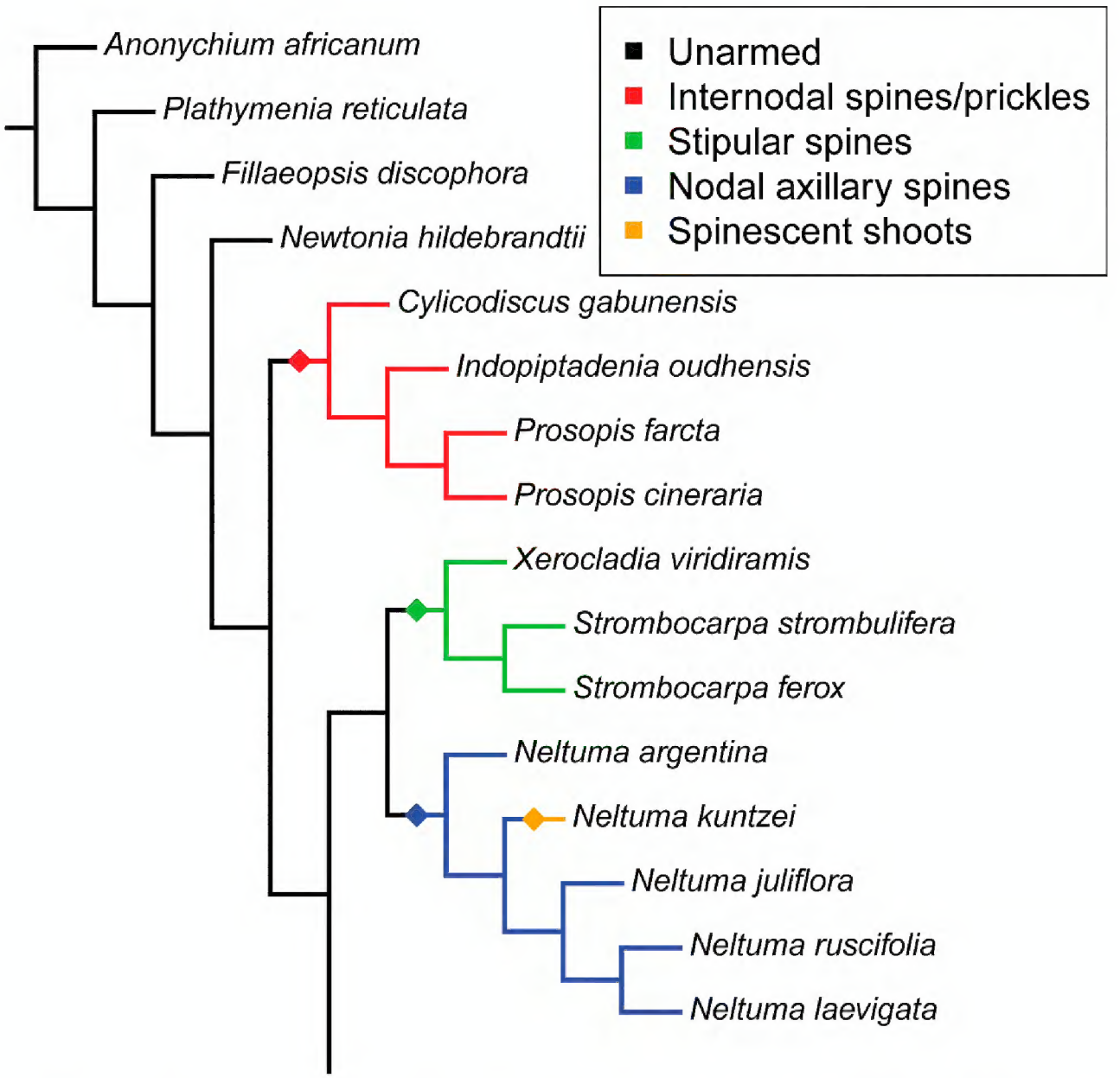

Figure 4. Independent evolutionary origins of stipular spines, axillary nodal spines and internodal spines across the segregate genera of the *Prosopis* s.l. grade. Diamonds indicate putative origins halfway along the branch subtending the clade with the character of interest. Note that, in the case of *Neltuma kuntzei*, a loss of axillary nodal spines, which are absent in that species, apparently coincides with an evolutionary gain of spinescent shoots (see also Fig. 3F) and with a shift to a largely aphyllous condition on the mature shoots. The reconstruction of armature characters shown here encompasses results of four independent optimisations of four types of armature, performed using the make.simmap option of R (R Core Team 2021) package phytools (Revell 2012), each with 500 simulations using the ARD model. Optimisations were performed on an ASTRAL phylogeny of the entire Caesalpinioideae, based on 821 single-copy genes (Ringelberg et al. 2022), but are here shown only for the *Prosopis* s.l. grade with standardised branch lengths.

by the contrast between the cylindrical or sub-cylindrical thickened indehiscent fruits of *Prosopis* s.l. (albeit varying considerably in the degree to which they are curved or coiled (see below)) and the very different plano-compressed fruits of *Indopiptadenia* (Figs 5M and 7B; see also Bajpai et al. 2014: Fig. 7), which is sister to section *Prosopis* and which lacks a thickened mesocarp and is dehiscent along one or both sutures. Similarly, *Xerocladia*, which is sister to section *Strombocarpa* (Fig. 1), has equally distinctive small reniform to flabellate, flattened, indehiscent, 1 (–2)-seeded, winged fruits,

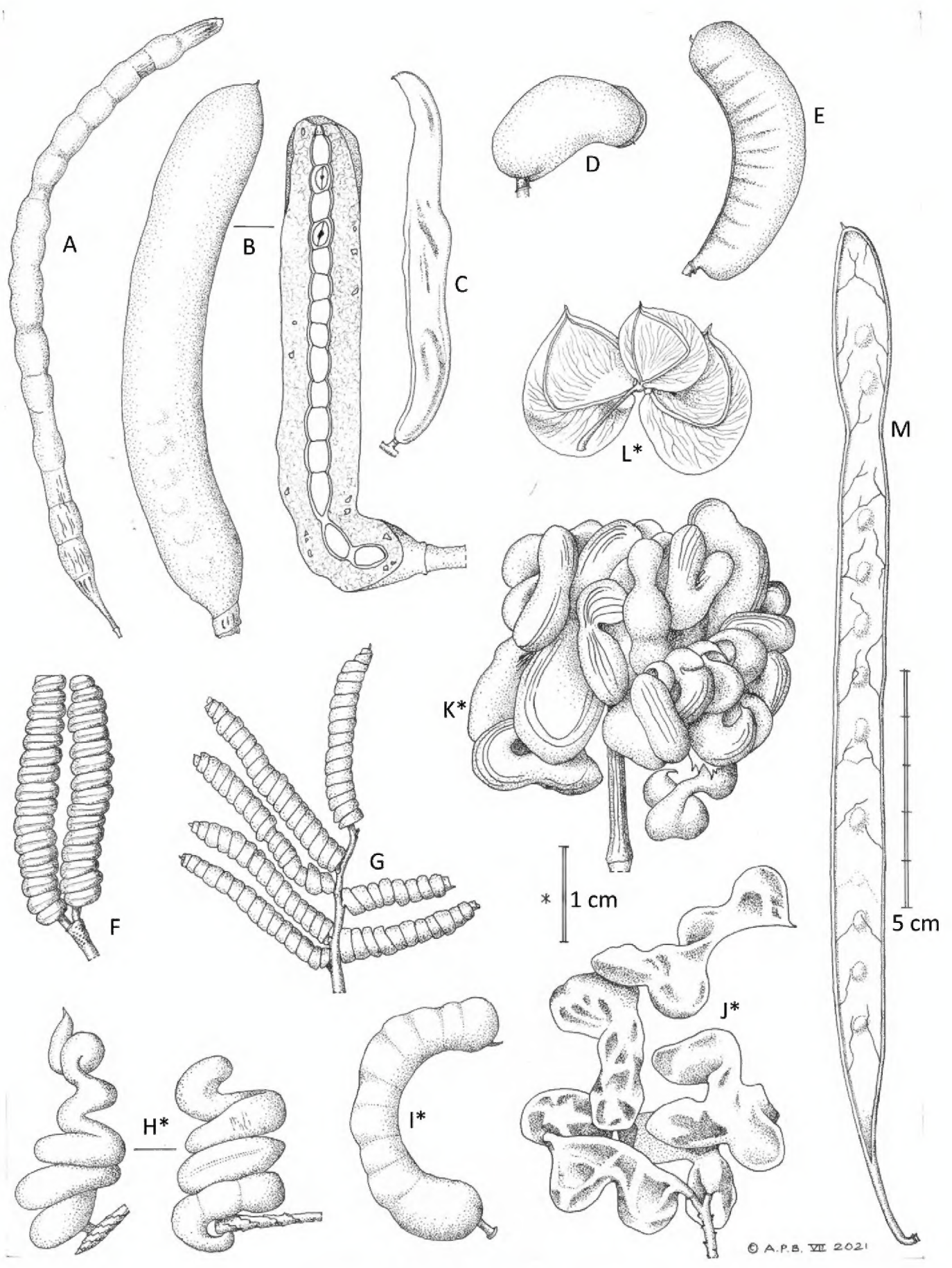

Figure 5. Fruits of *Prosopis*, *Strombocarpa*, *Xerocladia* and *Indopiptadenia* **A** *Prosopis cineraria* **B** *Anonychium africanum* **C** *Strombocarpa palmeri* **D** *Prosopis farcta* **E** *Strombocarpa ferox* **F** *S. strombulifera* **G** *S. pubescens* **H** *S. abbreviata* (2 examples) **I** *S. tamarugo* **J** *S. torquata* **K** *S. burkartii* **L** *Xerocladia viridiramis* **M** *Indopiptadenia oudhensis* **A-G, M** (5 cm scale bar) **H-L** (1 cm scale bar with asterisk). All specimens at K **A** drawn from *Gazanfar* SG4332 **B** *Dembele & Sanogo* ML-146 and longitudinal section of fruit from *Barter* 1193 **C** *Hughes et al.* 1552 **D** *van der Maesen* 1627 **E** *Atahuachi et al.* MA1147 **F** *Hunziker* 2036 **G** *Acocks* 1788 **H** *Tweedie* s.n. (from 2 type specimens) **I** *Aronson* 7742 **J** *Vuilleumier* 1019 **K** *Acosta & Rosas* 748 **L** *Kolberg & Tholkes* HK2493 **M** *Bajpai & Babu* 264498. Drawn by Andrew Brown, July 2021.

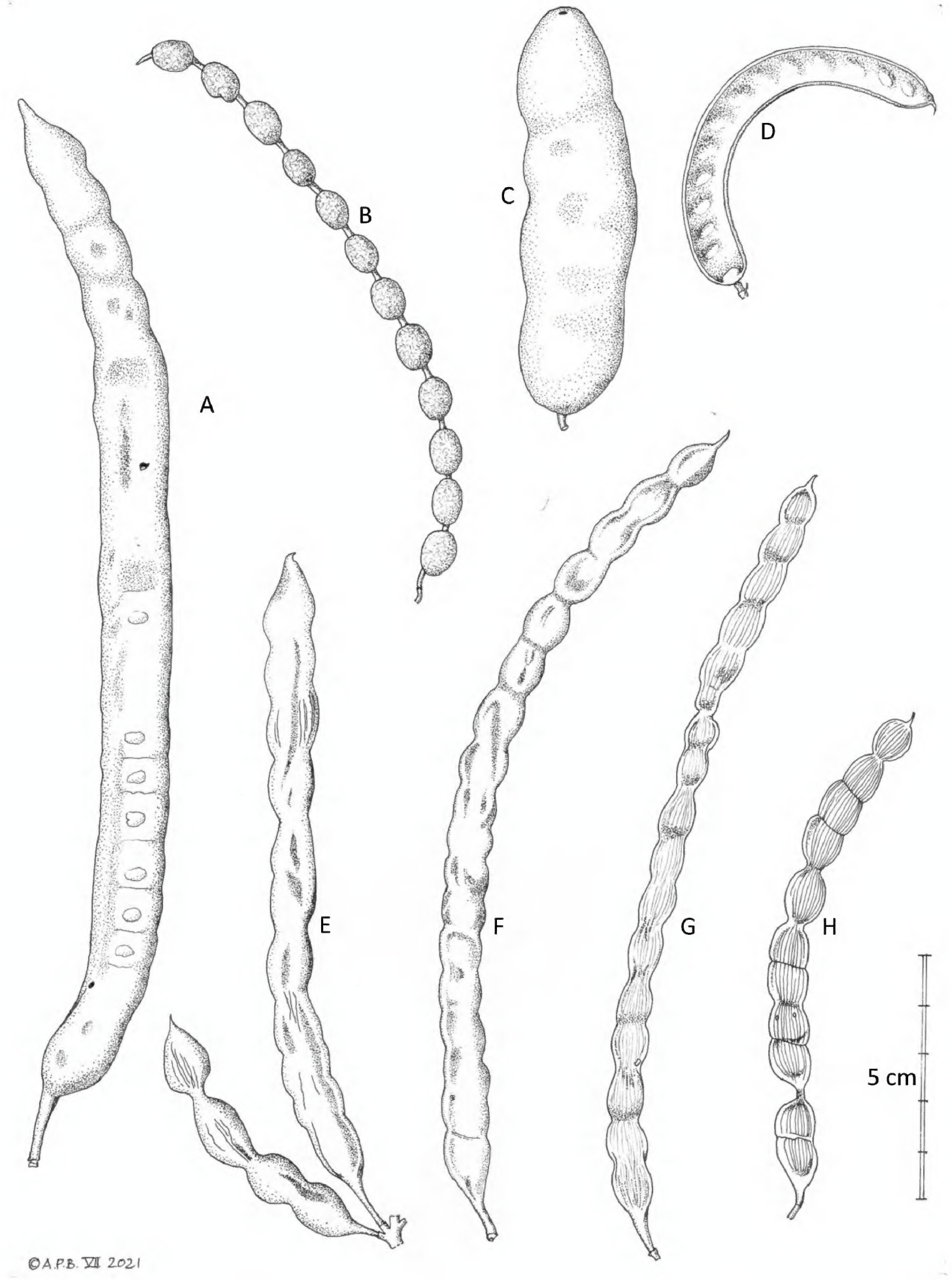

Figure 6. Fruits of *Neltuma* **A** *Neltuma alba* **B** *N. argentina* **C** *N. kuntzei* **D** *N. denudans* **E** *N. laevigata* **F** *N. nigra* **G** *N. articulata* **H** *N. ruscifolia*.(5 cm scale bar). All specimens at K **A** drawn from *Hughes & Forrest* 2312 **B** *Guaglianone et al.* 1762 **C** *Nee & Coimbra* 35556 **D** *Seijo* 1489 **E** *Manríquez & Tenorio* 6563 **F** *Arenas* 3123 **G** *Hughes et al.* 1559 **H** *Wood & Mamani* 14063. Drawn by Andrew Brown, July 2021.

Figure 7. Variation in fruits across *Prosopis* s.l. and allies **A** indehiscent pods of *Anonychium africanum* with thick pulpy mesocarp collected as fodder for livestock **B** plano-compressed pods of *Indopiptadenia oudhensis* lacking a thickened mesocarp and dehiscent along both sutures **C** indehiscent fruits of *Prosopis farcta* with a thick pulpy mesocarp **D** tightly coiled indehiscent screwbean fruits of *Strombocarpa strombulifera* **E** indehiscent pods of *Strombocarpa ferox* with a thick pulpy mesocarp **F** indehiscent fruits of *Strombocarpa palmeri* **G** small reniform to flabellate, flattened, indehiscent, 1 (–2)-seeded, winged fruits of *Xerocladia viridiramis* which are unique within mimosoid legumes **H** indehiscent fruits of *Neltuma articulata* with a thick mesocarp and a hard bony segmented endocarp which remains closed **I.** Unripe indehiscent pods of *Neltuma kuntzei* with a thick pulpy mesocarp, these turning dark blackish-brown when ripe, reminiscent in colour to fruits of *Anonychium*. Photos courtesy of Marco Schmidt (**A**) (see Dressler et al. 2014), Dr. Omesh Bajpai and Dr. Lal Babu Chaudhary (**B**), Zeynel Cebeci (**C**) (https//en.wikipedia.org/wiki/Prosopis_farcta), Dick Culbert (**D**) (see https//eol.org/pages/640506, Colin Hughes (**E, F, H, I**), and Herta Kolberg (**G**) (see Plants of Namibia https//herbaria.plants.ox.ac.uk/bol/namibia).

which are unique amongst mimosoid legumes as a whole (Figs 5L and 7G) and also lack the often-thick mesocarp of *Prosopis* s.l. fruits (Gunn 1984). Thus, it is now clear that the thickened, sub-cylindrical fruits of *P. africana* (section *Anonychium*), which are

superficially very similar (both are thick, woody, indehiscent and black when mature) to those of distantly related *P. kuntzei* Harms (section *Algarobia*) (Figs 5B, 6C, 7A, I), represent homoplasious evolutionary origins of similar endozoochorous seed dispersal syndromes, based on animal ingestion of highly palatable fruits and defecation of the seeds (Tybirk 1991; Weber et al. 2008) and, hence, are misleading as the basis for generic delimitation. In the light of phylogenetic data, it is now clear that Burkart's (1976) reliance on fruit morphology to unite his broad concept of *Prosopis* and demotion of armature as only useful at sub-generic rank and not for delimiting genera were misplaced.

It is notable that pollen exine structure also supports these groups. Pollen of the Old World species of section *Prosopis* is similar to that of its sister genus *Indopiptadenia*, showing a relatively thin (0.7–0.9 μm) tectum with irregularly areolate-verrucose raised sculpturing, whereas the New World species of *Prosopis*, and *Xerocladia* have a smooth (perforated) and even thinner (< 0.7 μm) tectum (Hernández and Guinet 1990: Fig. 5).

The type species of *Prosopis*, *P. spicigera* L. (a synonym of *P. cineraria* (L.) Druce), is from the Old World in section *Prosopis* of Burkart (1976), a clade that comprises just three of the 56 species currently recognised in the genus as a whole, implying that the remaining 53 species will require a name change to deal with the non-monophyly of *Prosopis* s.l. Segregation of the isolated monospecific lineage *P. africana* as a separate genus presents a straightforward and uncontroversial adjustment, here implemented by re-instatement of the genus *Anonychium* (Benth.) Schweinf. (see below). Generic re-delimitation of the New World species is less straightforward and is complicated by placement of the morphologically distinctive Namibian/Namaqualand monospecific genus *Xerocladia* nested within the New World *Prosopis* clade as sister to section *Strombocarpa* (Fig. 1). Despite its similar shrubby, multi-stemmed, branchy habit, green shoots, stipular spines (Fig. 3D) (shared with section *Strombocarpa*) and occurrence in arid succulent-rich vegetation, all of which are shared with New World *Prosopis*, the genus *Xerocladia* has been maintained as distinct from *Prosopis*, because it has highly distinctive reniform to flabellate, indehiscent, 1(–2)-seeded, winged fruits (Figs 5L and 7G), lacking a thickened mesocarp, which are very different from those of *Prosopis* s.l. and, indeed, from all other mimosoid legumes. Given this distinctive morphology, we retain *Xerocladia* as a separate genus. We also note that the material referred to under the name *Xerocladia pampeana* Speg. from Argentina, shows clear affinities to the genus *Prosopidastrum* Burkart, as suggested by Palacios and Hoc (2005). Even though Palacios and Hoc (2005) left *X. pampeana* as an excluded name in their treatment of Argentinian *Prosopidastrum*, examination of the material cited by them suggests that the fruits are not monospermous, but simply broken fragments of lomentiform fruits of *Prosopidastrum*.

Retention of the monospecific African *Xerocladia* at generic rank implies that the two subclades of New World *Prosopis* species, corresponding to Sections *Strombocarpa* and *Monilicarpa* + *Algarobia* of Burkart (1976) (Fig. 1), also need to be recognised as separate genera. Both of these groups have been previously ranked as genera. Bentham (1839), prior to uniting the various elements of *Prosopis* s.l. in a single genus in his

1875 treatment of Mimoseae, recognised section *Algarobia* at generic rank as the genus *Algarobia* Benth. (even though the name *Algarobia* is preceded by *Neltuma* Raf. published one year earlier in 1838). Similarly, section *Strombocarpa* was also afforded generic status as the genus *Strombocarpa* Englm. & A. Gray in 1845, a generic delimitation followed by Britton & Rose (1928) in their treatment for the North America Flora. The alternative to recognising these two New World clades as separate genera would be to transfer all New World species of *Prosopis* plus the African *Xerocladia* to the genus *Neltuma*. While it could be argued that this alternative would make generic-level identification in the New World easier, it would entail lumping *Xerocladia* with its highly unusual fruits which are unique within mimosoids and would detract from the overall ability to diagnose genera across mimosoids. We believe that upranking Burkart's sections *Strombocarpa* and *Algarobia* + *Monilicarpa* as the genera *Strombocarpa* and *Neltuma*, respectively, distinguished by the differences in armature that provided the basis for Burkart's sections, while retaining the African *Xerocladia* as a separate genus (Fig. 1), provides the best solution to render all genera monophyletic and ensure maximal ability to diagnose genera across mimosoids as a whole.

Finally, for completeness, we note that the genus *Sopropis* Britton & Rose, erected by Britton & Rose (1928) to accommodate the somewhat unusual species *Sopropis palmeri* (S. Watson) Britton & Rose (= *Prosopis palmeri* S. Watson) has the stipular spines of section *Strombocarpa*, but a straight (or only weakly falcate) fruit more typical of section *Algarobia* (Figs 5C and 7F), as noted by Benson (1941). In the phylogeny of Catalano et al. (2008), *P. palmeri* is placed in the clade corresponding to section *Strombocarpa* with robust support, vindicating the congruence of armature types across the phylogeny and we here treat *Sopropis* as a synonym of *Strombocarpa*. This is very much in line with Burkart's (1976) view that too much weight had been given by Britton and Rose (1928) to the curvature and coiling of the *Prosopis* fruit in the recognition of three distinct genera in their Flora of North America treatment. Indeed, it is clear that curvature of the pod across New World *Prosopis* s.l. shows a continuum from the tightly spirally coiled 'screwbean' pods of, for example, *P. strombulifera* (Lam.) Benth. and *P. pubescens* Benth. (Figs 5F, G and 7D), to fruits with fewer, larger and more open coils, annular fruits and those that are only weakly curved or completely straight, variation that is discordant with sectional boundaries (Figs 5B, C, E–K, 6 and 7D–F, H–I) and with the phylogeny (Fig. 1).

Taxonomic name changes are often unwelcome for many users, at least in the short term, especially for plant groups that are important ecologically and in terms of human uses. This is very much the case for *Prosopis* s.l. and especially so in the warm desert and dryland scrub ecosystems of the New World, where "few plant genera have received as much attention as *Prosopis*" (Simpson 1977: ix). Species of *Prosopis* are ecologically abundant in many parts of its New World range, dominating vast tracts of the Chaco in South America and the matorrales of the southern U.S.A. and parts of Mexico (Fig. 8) (Benson 1941). Trees of *Prosopis* s.l. also occupy a central place in silvo-pastoral systems more widely across the arid and semi-arid tropics from Rajasthan in NW India, through the Arabian Peninsula, across Sahelian Africa and

throughout the arid zones of the Neotropics (Leakey and Last 1980; Fagg and Stewart 1994; Pasiecznik et al. 2001; Weber et al. 2008), because of their dependable provision of abundant protein- and sugar-rich, non-toxic, highly palatable and nutritious fruits during the dry season that are eagerly consumed by diverse livestock (cattle, sheep, goats, camelids). Furthermore, *Prosopis* s.l. fruits, including the *mezquites* in North America (Felger 1977) and the *algorrobos* in South America (D'Antoni and Solbrig 1977), constituted one of the most important wild food sources for pre-hispanic cultures, with *P. velutina* Wooton, the velvet mesquite referred to as the 'tree of life' (Bell and Castetter 1937) and these uses potentially prompting long distance translocation of species by humans and their livestock within the Americas in pre-Colombian times (McRostie et al. 2017). In addition to livestock fodder and human food, the wood of *Prosopis* is dense and durable and widely used for firewood, charcoal and parquet flooring and the flowers provide high quality, reliable and abundant forage for honey bees. Moreover, such is the ability of some *Prosopis* species to disperse seeds, colonise and quickly form dense spiny impenetrable thickets, that some species of *Prosopis* are amongst the world's worst invasive weeds, both within and well beyond their native ranges. For example, several New World section *Algarobia* species are naturalised and invasive across many parts of Africa, the Middle East, the Indian subcontinent and Australia (e.g. Pasiecznik et al. 2001; Van Klinken and Campbell 2001; Ayanu et al. 2015) and have been recorded from 103 countries and considered to be invasives in 49 of those (Shackleton et al. 2014). Within their native distributions, *P. ruscifolia* Griseb. is a serious pest in the western Gran Chaco, referred to as a '*plaga nacional*' and *P. glandulosa* Torr. has prompted the so-called '*mesquite problem*' in Texas in the southern U.S.A. where that species is considered a serious rangeland weed (Fisher et al. 1959).

The impacts of name changes on a group of plants of such diverse importance cannot be denied and, inevitably, we anticipate resistance, in the short term, to the nomenclatural changes we propose here. Notwithstanding, we also expect that, ultimately, there will be benefits from aligning genera with monophyletic groups that more accurately reflect their evolutionary placements and provide a deeper biological understanding of these globally-important plants. In that light, it is notable that all the serious invasive and rangeland pest species fall into *Neltuma* (= section *Algarobia*), suggesting that a propensity for invasiveness is more problematic for species in that clade. Similarly, of 29 species of bruchid beetles known to predate seeds of New World *Prosopis*, only two span *Neltuma* (sections *Algarobia* + *Monilicarpa*) and *Strombocarpa*, such that each of the two New World clades has largely its own exclusive bruchid fauna, including, for example, the bruchid genus *Algarobius* Bridwell which is largely restricted to species of section *Algarobia* (Kingsolver et al. 1977). More generally, biocontrol programmes to mitigate invasions of New World species of *Neltuma* in Africa have focused on insects, such as the bruchid seed predator *Algorobius prosopis* (J.L. Leconte), that do not attack native African members of *Prosopis* s.l. including species of *Prosopis* s.s., *Anonychium* and *Xerocladia*, suggesting that many insects effectively distinguish amongst the genera proposed here (Kleinjan et al. 2021).

It is also notable that, while intra-sectional interspecific hybridisation has been reported to occur in both section *Strombocarpa* (e.g., the hybrid origin of *Prosopis burkartii* Muñoz, Contreras et al. 2020) and amongst a subset of species in the 'mesquite clade' of *Neltuma* (= sections *Algarobia* + *Monilicarpa*) (Hunziker et al. 1986; Castillo et al. 2021), there are no examples of inter-sectional hybrids between species belonging to *Neltuma* and *Strombocarpa* (Solbrig et al. 1977; Hunziker et al. 1986), despite their sympatry across many areas (Fig. 8). This lack of inter-sectional crossing prompted Hunziker et al. (1986) to suggest upranking sections *Algarobia* (= *Neltuma*) and *Strombocarpa* "at least to the level of subgenera", as also suggested by Saidman et al. (1996), based on genetic differences. Similarly, phylogenetic analysis of morphology and biochemical traits showed strong support for recognising *Strombocarpa* as a distinct clade (Burghardt and Espert 2007). These trait differences, alongside other ecological differences, are symptomatic of the deep (phylo)genetic split between these two clades which are estimated to have diverged 25 Myr (Ringelberg et al., in prep). All these differences in biology are of potential significance for genetic improvement, range management and biocontrol programmes (see Kleinjan et al. 2021), adding further justification to recognise Burkart's sections at generic rank.

Biogeography

One of the uniting features of *Prosopis* s.l. is the distribution of its various lineages, first and foremost, in seasonally dry and arid tropical and subtropical climates across the New and Old Worlds (Fig. 8), a distribution that spans, in large part, the transcontinental grass-poor succulent-rich, fire-free succulent biome sensu Schrire et al. (2005) and Ringelberg et al. (2020). However, in that sense, *Anonychium* (*P. africana*) is an outlier, just as it is phylogenetically, because it grows in savannahs across Sahelian Africa. The *Prosopis* s.s. + *Indopiptadenia* clade spans an interesting dry/monsoonal west-central Asian distribution which is unique amongst mimosoids. At first sight, the sister group relationship between *Strombocarpa* and *Xerocladia* spanning the Atlantic seems a surprising disjunction, but several other Caesalpinioid legumes show similar disjunct amphi-Atlantic distributions with most of their diversity in the Neotropics and outlying endemic species in Namibia and adjacent regions of southern Africa. These include the genera *Haematoxylum* L., *Parkinsonia* L. and *Pomaria* Cav., with *Haematoxylum dinteri* Harms, *Parkinsonia africana* Sond. and three species of *Pomaria* in Namibia and S. Africa. Two things are notable about these transatlantic disjunctions. First, they often show bicentric amphitropical ranges in the New World and disjunctions in SW Africa (the *Haematoxylum* + *Lophocarpinia* Burkart clade; *Pomaria* (Simpson et al. 2006); *Strombocarpa* - *Xerocladia*). Second, they share similar seasonally dry tropical, grass-poor, succulent-rich, fire-free ecologies across the transcontinental Succulent Biome (Schrire et al. 2005; Gagnon et al. 2019; Ringelberg et al. 2020).

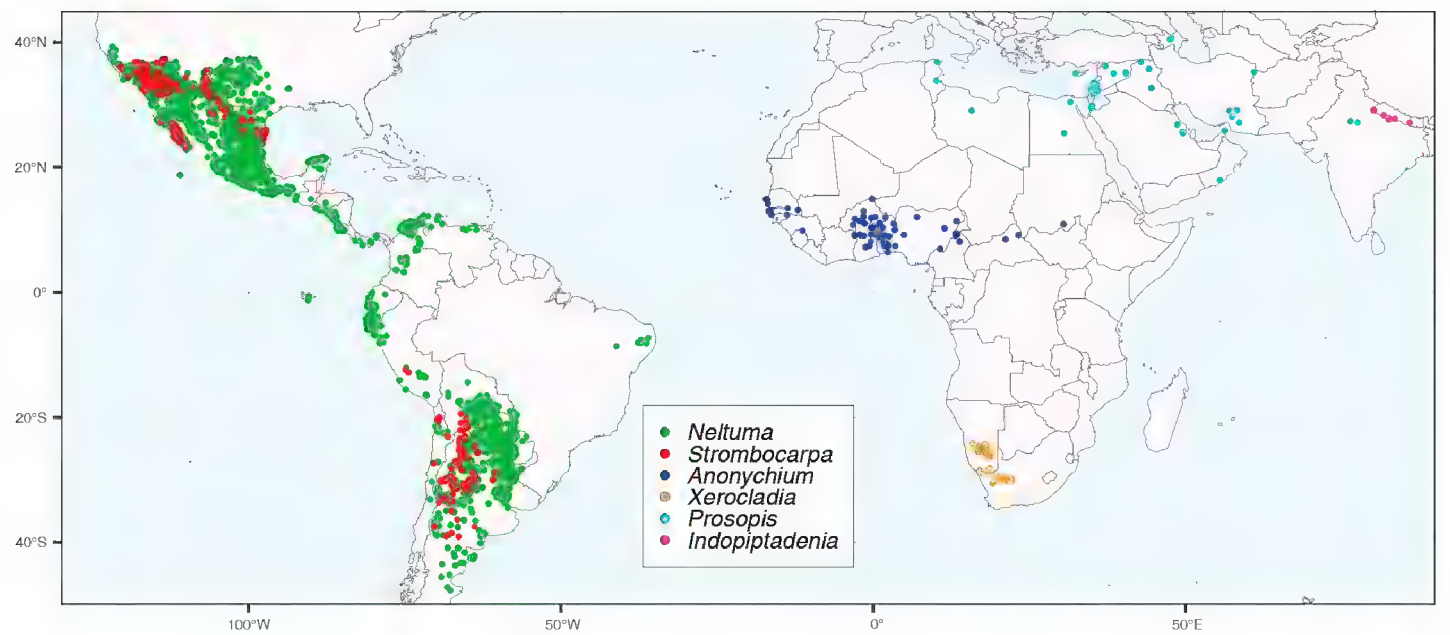

Figure 8. The distributions of *Indopiptadenia*, *Prosopis* s.s., *Anonychium*, *Xerocladia*, *Neltuma* and *Strombocarpa*, based on 6,469 quality-controlled species occurrences from GBIF (www.gbif.org), DryFlor (www.dryflor.info), SEINet (www.swbiodiversity.org/seinet) and several other data sources (Ringelberg et al., in prep.). Map created using R packages ggplot2 (Wickham 2016), sf (Pebesma 2018) and rnaturalearth (South 2017). The eight occurrence records, mapped in Bahia Brazil, are of *Neltuma ruscifolia* which is considered potentially native to that region (Burkart 1976 Oliveira & Queiroz 2020), while records of *N. juliflora* from Bahia, which is introduced and naturalised in that region, have been eliminated.

Key for the identification of the segregate genera of *Prosopis* and close allies (see Figs 2 and 3 for illustrations of armature characters used in the key)

1	Plants unarmed	***Anonychium***
–	Plants usually armed with stipular spines, axillary solitary or paired uninodal cauline spines, spinescent shoots or internodal prickles	**2**
2	Plants armed with internodal prickles on shoots and/or stems, petals glabrous	**3**
–	Plants armed with stipular spines, axillary solitary or paired uninodal spines or spinescent shoots, petals villous or pilose	**4**
3	Fruits indehiscent, cylindrical or subterete, with a pulpy or fibrous mesocarp, largest leaflets < 1.5 × 1 cm, mature stems with scattered prickles	***Prosopis***
–	Fruits dehiscent, plano-compressed, coriaceous, lacking a thick mesocarp, larger leaflets > 3 × 3 cm, mature stems with spine-tipped woody protuberances	***Indopiptadenia***
4	Fruits reniform to flabellate, indehiscent, 1–2-seeded and winged	***Xerocladia***
–	Fruits linear or oblong, always > 2-seeded	**5**
5	Plants armed with stipular spines	***Strombocarpa***
–	Plants armed with axillary, uninodal, solitary or paired spines or spinescent shoots	***Neltuma***

Taxonomy

We present a taxonomic synopsis of the four segregate genera, *Anonychium*, *Prosopis*, *Strombocarpa* and *Neltuma*, including 57 new nomenclatural combinations and associated synonymy. Type details are cited for accepted names, but not for heterotypic synonyms.

Anonychium (Benth.) Schweinf., Reliq. Kotschy.: 7. 1868.

Prosopis section *Anonychium*, Benth. Hook. J. Bot. 4: 347. 1842.

Type. *Prosopis oblonga* Benth. Benth., J. Bot. (Hooker) 4: 348. 1842, a synonym of *Anonychium africanum*.

Description. Unarmed trees 4–20 m high, branches lacking axillary brachyblasts. Stipules inconspicuous, long-lanceolate, pubescent, caducous as young leaves develop, absent from most herbarium sheets. Leaves somewhat pendulous, 1–4 pairs of pinnae, the petiole 3–5 cm long, the rachis 5–9 cm long, the pinnular rachises 6–15 cm long, with 4–13 pairs of opposite leaflets, these 1.3–3.5 × 0.4–1.5 cm, glabrous or finely pubescent, mid-vein subcentric. Inflorescences spicate, 5–9 cm long, axillary, solitary or in pairs, densely flowered; pedicels 0.5 mm. Flowers small, yellowish or greenish-white, sweetly scented; calyx ca. 1 mm long; corolla ca. 3.5 mm long, the petals linear, free, glabrous on both sides; anthers apically broadened with an unusual anther gland borne ventrally between the thecae and forming a triangular hood-shaped protrusion made up of papillate cells; pollen with costae on the pores and a smooth (perforated) tectum; ovary and style pilose or villous. Fruits indehiscent, straight or sub-falcate, dark reddish-brown to blackish, shiny, subterete, 10–20 × 1.5–3.3 cm, exocarp hard, 1–2 mm thick, mesocarp spongy, thick, dry, endocarp segments thin, longitudinal, in one row (Figs 5B and 7A). Seeds many, dark, shiny, ovate compressed, 8–10 × 4–9 mm, rattling within the pod when ripe.

Geographic distribution. Monospecific. Widespread across Sahelian Africa, from Senegal in the west to Sudan and Ethiopia in the east (Fig. 8).

Habitat and uses. *Anonychium africanum* is native across the whole Sahelian savannah belt. Trees are maintained and managed by farming and pastoralist communities in traditional silvo-pastoral systems throughout the African Sahel, providing essential products, including wood, fuel, food, livestock fodder and medicines and enhancing soil fertility (Weber et al. 2008). Seeds are widely dispersed by browsing animals, such as camels, cattle and goats at the end of the dry season (Tybirk 1991) and perhaps also by humans who collect the pods to feed to their animals, and cow dung (containing viable seeds) to fertilise their fields.

Etymology. *Anonychium* literally meaning the absence of nails or claws from the Latin or Greek 'onych' = 'ónyx' meaning nail or claw, refers to the lack of armature of this genus.

Affinities. *Prosopis africana* has long been considered anomalous within the genus and was placed in its own section *Anonychium* by Bentham (1842) and later this was upranked to its own genus, *Anonychium* by Schweinfurth (1868; under the name *A. lanceolatum* Schweinf.). Unlike almost all other species of *Prosopis* s.l., *P. africana* lacks armature, has internally glabrous petals, pollen with costae (Guinet 1969), V-shaped anthers with small stomia forming short pockets on the ventral surface of the anthers and anther glands that are apparently morphologically unique within mimosoids (Luckow and Grimes 1997). The anther glands of *Anonychium africanum* (as *P. africana*, Luckow and Grimes 1997: Figs 25–27) stand out as quite different from the typical mimosoid claviform anther glands of the remaining species of *Prosopis* s.l., being sessile, borne ventrally between the thecae, rather than stipitate borne apically or dorsally from the connective between the thecae as in most other mimosoids and forming triangular hood-shaped protrusions made up of papillate cells which are also unique amongst mimosoid anther glands (Luckow and Grimes 1997). Alongside the robust molecular evidence for placement of *P. africana* distantly related to the rest of *Prosopis* (Fig. 1), this suite of morphological differences amply justifies segregation of *P. africana* as a distinct monospecific genus.

Anonychium is a phylogenetically isolated lineage that subtends the grade of other unarmed, mainly species-poor genera, *Plathymenia*, *Fillaeopsis* and *Newtonia* which is paraphyletic with respect to the core mimosoid clade of Koenen et al. (2020) (Fig. 1; Ringelberg et al. 2022). This is in line with pollen of *Anonychium* which shows similarities to *Newtonia* (Guinet 1969).

***Anonychium africanum* (Guill. & Perr.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303578-1

Prosopis oblonga Benth., J. Bot. (Hooker) 4: 348. 1842.
Entada durissima Baill., Adansonia 6: 208. 1866.
Anonychium lanceolatum Schweinf., Reliq. Kotschy.: 7, pl. 7. 1868.
Prosopis africana (Guill. & Perr.) Taub. in H.G.A. Engler & K.A.E. Prantl, Nat. Pflanzenfam. 3(3): 119. 1892.
Entada coulteri Roberty, Bull. Inst. Fondam. Afrique Noire, Sér. A, Sci. Nat. 16: 346. 1954.

Basionym. *Coulteria africana* Guill. & Perr., Fl. Seneg. Tent.: 256, 1832.

Type material. Senegal. Kounoun, Presqu'île du Cap-Vert, *G.S. Perrottet 20* (holotype: P [P00418356]).

***Prosopis* L., Mantissa Pl. 68: 10. 1767. emend. C.E. Hughes & G.P. Lewis.**

Lagonychium M. Bieb., Fl. Taur.-Caucas. 3: 288. 1819.
Prosopis section *Adenopis* DC., Prodr. 2: 446. 1825.
Pleuromenes Raf., Sylva Tellur.: 144. 1838.

Type. *Prosopis spicigera* L., a synonym of *P. cineraria* (L.) Druce.

Description. Prickly subshrubs, shrubs, small trees or occasionally lianescent (*P. farcta*), 0.3–6.5 (–10) m high, deep-rooted and sometimes invading via root suckers, prickles internodal, scattered, straight, somewhat acroscopic, conical with broad bases, 3–5 mm long (Figs 2C, M and 3C), stipular or axillary spines absent. Stipules foliaceous, ovate-acute, caducous. Leaves with 1–6 (–7) pairs of pinnae, the petiole and rachis 0.5–4 cm, sometimes a prickle at the base of the petiole, the pinnular rachises 2–7 cm long, with 7–15 pairs of leaflets, these ovate or lanceolate, straight to sub-falcate or auriculate, mucronate, 2–15 × 2–4.5 mm, glabrous, puberulous or pubescent, mid-vein excentric. Inflorescences spicate, 4–13 cm long, axillary, solitary or in fascicles, peduncle sometimes with an amplexicaul bract, this caducous and leaving an oblique scar; pedicels 0.5–1.5 mm. Flowers small, yellow, yellowish-white, green or cream-green; calyx truncate, 0.8–1.2 mm long; corolla 3.5–4 mm long, the petals linear, nearly free, reflexed, glabrous on both sides; anthers with a minute caducous incurved claviform gland arising from the connective; pollen lacking costae on the pores, tectum irregularly areolate-verrucose. Fruits indehiscent, slender, elongate straight or sub-falcate, dark reddish-brown to blackish, shiny, cylindrical to sub-cylindrical, torulose, 1.5–19 × 0.4–2.5 cm, exocarp thin, brittle, shiny and smooth, orange-red becoming brown, red or black when ripe (Fig. 7C), mesocarp spongy, endocarp segments thin, little developed, seed chambers longitudinal or transverse. Seeds well separated, longitudinal, ovate to ovoid, compressed, 6–8.5 × 5–6 × 2.5–3 mm.

Geographic distribution. Reduced now to just three Old World species, these distributed across arid parts of North Africa (but apparently the genus rare at its western limits in Algeria and Tunisia), the Middle East and NW India (especially Punjab and Rajasthan) and reaching its northern limits in Afghanistan and Azerbaijan (Fig. 8).

Habitat and uses. Abundant in dry and arid parts of NW India, where it is sometimes the most common tree in parts of Punjab and Rajasthan and abundant in arid thorn scrub in parts of the Near East (where *P. farcta*, which can spread via root suckers, is sometimes considered weedy), tolerating saline soils. Highly valued as a source of high quality durable wood, pods for livestock feed and bee forage.

Etymology. Pasiecznick et al. (2001) suggested the name to be derived from *pros-* (Gk.: towards) and *Opis* (wife of Saturn, the Greek goddess of abundance and agriculture), hence 'towards agriculture' referring to the widespread utility of the genus.

Affinities. *Prosopis* s.s. is here reduced to three species and is sister to the monospecific genus *Indopiptadenia* (Fig. 1). These two genera share stem/internodal prickles and a W-C Asian distribution that is unique within mimosoids.

***Prosopis cineraria* (L.) Druce, Rep. Bot. Exch. Club Soc. Brit. Isles 3: 422. 1913. (publ. 1914).**

Mimosa cinerea L., pro parte, Sp. Pl.: 517. 1753 (see note below).
Prosopis spicigera L., Mant. Pl.: 68. 1767.
Prosopis spicata Burm.f., Fl. Indica: 102. 1768.

Prosopis aculeata J. Koenig ex Roxb., Asiat. Res. 4: 405. 1795.
Adenanthera aculeata (J. Koenig ex Roxb.) W. Hunter, Asiat. Res. 6: 66. 1799.
Acacia cineraria (L.) Willd., Sp. Pl., ed. 4, 4: 1057. 1806.

Note. The name *Mimosa cineraria* L. (Syst. Nat., ed. 10: 1311. 1759), based on *M. cinerea* L. (Sp. Pl.: 517 [non 520]. 1753; see Art. 53 Ex. 19), was transferred to *Prosopis* L. by Druce (in Bot. Exch. Club Brit. Isles Rep. 3: 422. 1914) as *P. cineraria* (L.) Druce. However, the correct name in *Prosopis* would have been a combination based on *M. cinerea* (l.c.) had not that name been successfully proposed for rejection (see App. V). in ICN Art. 53.5, Note 4.

Type material. India.

***Prosopis farcta* (Banks & Sol.) J.F. Macbr., Contr. Gray Herb. 59: 17. 1919.**

Mimosa farcta Banks & Sol. in A. Russell, Nat. Hist. Aleppo, ed. 2, 2: 266. 1794.
Mimosa stephaniana M. Bieb., Tabl. Prov. Mer Casp.: 120. 1798.
Acacia stephaniana (M. Bieb.) Willd., Sp. Pl., ed. 4, 4: 1088. 1806.
Acacia heterocarpa Delile, Descr. Egypte, Hist. Nat.: 79. 1813.
Lagonychium stephanianum (M. Bieb.) M. Bieb., Fl. Taur.-Caucas. 3: 288. 1819.
Mimosa arvensis Sieber ex Steud., Nomencl. Bot. 1: 533. 1821, nom invalid.
Prosopis stephaniana (M. Bieb.) Kunth ex Spreng., Syst. Veg. 2: 326. 1825.
Mimosa agrestis Sieber ex Spreng., Syst. Veg. 2: 206. 1825.
Pleuromenes heterocarpa Raf., Sylva Tellur.: 145. 1838.
Acacia persica Sterler ex Steud., Nomencl. Bot., ed. 2, 1: 7. 1840.
Mimosa micrantha Vahl ex Walp., Repert. Bot. Syst. 5: 582. 1846.
Lagonychium farctum (Banks & Sol.) Bobrov in V.L. Komarov (ed.), Fl. URSS 11: 14. 1941.
Prosopis farcta var. *glabra* Burkart, J. Arnold Arbor. 57: 454. 1976.

Type material. Syria. Aleppo, without collector; no additional information in protologue.

***Prosopis koelziana* Burkart, J. Arnold Arbor. 57: 455. 1976.**

Prosopis koelziana var. *puberula* J. Léonard, Bull. Jard. Bot. Natl. Belg. 56: 485. 1986.

Type material. Iran. Madenu, Kirman, *Koelz 14246* (holotype: US [US00000985]).

***Strombocarpa* (Benth.) Engelm. & A. Gray, Boston J. Nat. Hist. 5: 243. 1845.**

Spirolobium A.D. Orb., Voy. Amér. Mér. 8 (Atlas, Bot): t. 13. 1839, nom. rej., non *Spirolobium* Baill. 1889. (Apocynaceae).
Prosopis sect. *Strombocarpa* Benth., J. Bot. (Hooker) 4: 351. 1841.

Sopropis Britton & Rose in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 182. 1928.

Type. *Prosopis strombulifera* (Lam.) Benth. [= *Strombocarpa strombulifera* (Lam.) A. Gray].

Description. Low spiny, sometimes creeping, shrubs or small trees, 0.15–3 (–18) m high, multi-stemmed from the base or sometimes with a short trunk to 10–30 (–45) cm diameter, usually densely and intricately much-branched, some species forming long underground, spreading, horizontal runners (gemmiferous roots or rhizomes), armed with strongly decurrent, straight, cinereous spiny stipules (Figs 2E, H, I and 3A), 0.1–3.5 (–5.5) cm long, brachyblasts congested, blackish. Leaves always unijugate, the petiole (0.5–) 2–15 mm, the pinnular rachises 1–4 cm long, with 3–30 pairs of well separated, alternate to opposite leaflets, these oblong or elliptic-oblong, obtuse to subacute, veins lacking or weakly 1–3-veined, 2–12 × 0.6–4 mm, glaucous, puberulous or glabrescent. Inflorescences axillary, solitary, globose, ovoid-elliptic heads to 1.5 cm diameter at anthesis or shortly cylindrical-spicate, 3–8 cm long. Flowers small, bright or lemon yellow, young filaments red; calyx, 1.5–2.3 mm long; corolla 3–4 (–6) mm long, the petals linear, partially united, villous within; stamens and style exserted, anthers with a minute, caducous, incurved claviform gland arising from the connective. Fruits densely clustered with 1–21 per flower head, indehiscent, lemon-yellow, straw-yellow or reddish-brown when ripe, slender, elongate, straight or falcate (in *S. palmeri* and *S. ferox*; Figs 5C, E and 7E–F), but usually more or less tightly spirally coiled (like cork-screws) with (1–) 8–19 (–24) regular coils, forming a cylindrical body 1.8–5.5 × 0.6–1.5 cm (Figs 5F, G and 7D) or irregularly and more openly coiled; exocarp crustaceous, mesocarp thin or more usually thick and pulpy, tannic, reddish, endocarp delicately segmented in longitudinal or transverse seed chambers which are easy to open or hard and closed. Seeds ovate or reniform ovoid, grey-green, 3–6 (–7) × 3–4 mm.

Geographic distribution. Ten species. Restricted to the New World and there occupying a markedly bicentric amphitropical distribution in arid and semi-arid regions of N. America (southern U.S.A., especially in the Sonoran Desert, Baja California and northern Mexico (Coahuila)) and S. America (south-central Peru to Argentina and Chile) (Fig. 8).

Habitat and uses. In cactus-rich semi-desert Monte vegetation, deserts and arid mesetas, dry river beds and washes and in the hyper-arid Pampa del Tamarugal in northern Chile (*S. tamarugo*), where it is the only tree present and dependent on moisture absorbed from fog. Fruits browsed by cattle and sheep and much valued in arid deserts for that purpose. Wood valued for fuel, and occasionally cultivated (*S. tamarugo*).

Etymology. *Strombo-* (Italian. = conch) and *-carpa* (Gk. = fruit), referring to the resemblance of the fruits to the spiral shells of tropical marine molluscs (see Figs 5F, G and 7D).

Affinities. *Strombocarpa* is robustly supported in recent molecular phylogenies as sister to the African monospecific genus *Xerocladia* (Fig. 1; Ringelberg et al. 2022). These two genera share the diagnostic synapomorphy of stipular spines which are not found elsewhere in *Prosopis* s.l.

***Strombocarpa abbreviata* (Benth.) Hutch., Gen. Fl. Pl. 1: 287. 1964.**

Prosopis abbreviata Benth., J. Bot. (Hooker) 4: 352. 1842.

Type material. ?Argentina. "San Jago", *Tweedie 168* (holotype: K [K000504799]).

***Strombocarpa burkartii* (Muñoz) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303579-1

Basionym. *Prosopis burkartii* Muñoz, Bol. Mus. Nac. Hist. Nat., Santiago de Chile 32: 364. 1971.

Type material. Chile. Prov. Tarapacá, Pampa del Tamarugal, El Gobierno, sector La Huaica, *C. Muñoz Pizarro 7370* (holotype: SGO [SGO000002436]).

***Strombocarpa cinerascens* A. Gray, Smithsonian Contr. Knowl. 3(5): 61. 1852.**

Prosopis cinerascens (A. Gray) Benth., Trans. Linn. Soc. London 30: 381. 1875.
Prosopis reptans var. *cinerascens* (A. Gray) Burkart, Darwiniana 4: 75. 1940.
Prosopis reptans subsp. *cinerascens* (A. Gray) A.E. Murray, Kalmia 13: 24. 1983.
Mimosa calcarea Buckley, Proc. Acad. Nat. Sci. Philadelphia 1861: 453. 1862.

Type material. Mexico. Nuevo León ("New Leon"), valley near Azufrosa, *Gregg 492* (holotype: GH [GH00003469]; isotypes: K [K000791013], MO [MO356342]).

***Strombocarpa ferox* (Griseb.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303580-1

Basionym. *Prosopis ferox* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 118. 1879.

Type material. Argentina. "in regione Puna pr. Humaguaca, pr S José de Tilcara", Jujuy, Humahuaca, *P.G. Lorentz & G.H.E.W. Hieronymus 776* (lectotype: GOET [GOET009646]; isolectotypes: CORD [CORD00004889], F [F0BN001461], SI [SI002480]).

***Strombocarpa palmeri* (S. Watson) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303581-1

Basionym. *Prosopis palmeri* S. Watson, Proc. Amer. Acad. Arts 24: 48. 1889.

Sopropis palmeri (S. Watson) Britton & Rose in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 183. 1928.

Type material. Mexico. Eastern Baja California, Mulegé, *E. Palmer 2* (isotypes: BM [BM000952298], GH [GH00003471], K [K000478262], NDG [NDG24111], NY [NY00005123], US [US00930830]).

***Strombocarpa pubescens* (Benth.) A. Gray, Smithsonian Contr. Knowl. 3(5): 60. 1852.**

Prosopis pubescens Benth., London J. Bot. 5: 82. 1846.
Prosopis emoryi Torr. In W.H. Emory, Not. Milit. Reconn. 2: 189. 1848.
Strombocarpa brevifolia Nutt. ex A. Gray, Smithsonian Contr. Knowl. 3(5): 60. 1852.

Type material. U.S.A. California: between San Miguel and Monterey, *Coulter s.n.*

***Strombocarpa reptans* (Benth.) A. Gray, U.S. Expl. Exped., Phan. 1: 475. 1854.**

Prosopis reptans Benth., J. Bot. (Hooker) 4: 352. 1842.
Prosopis abbreviata var. *argentina* Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 133. 1874.

Type material. South America. with the label "Mortworta of Cordova, used as a cure for Dysentery" , *Tweedie s.n.* (K [K000504784]).

***Strombocarpa strombulifera* (Lam.) A. Gray, U.S. Expl. Exped., Phan. 1: 475. 1854.**

Mimosa strombulifera ("strumbulifera") Lam., Encycl. 1: 15. 1783.
Acacia strombulifera (Lam.) Willd., Sp. Pl., ed. 4, 4: 1055. 1806.
Prosopis strombulifera (Lam.) Benth., J. Bot. (Hooker) 4: 352. 1842.

Type material. Peru. no further details in protologue of *Mimosa strombulifera*.

***Strombocarpa strombulifera* var. *ruiziana* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303582-1

Basionym. *Prosopis strombulifera* var. *ruiziana* Burkart, J. Arnold Arbor. 57: 459. 1976.

Type material. Argentina. Mendoza: Dept. Junín, in aridis salsis inter Barrancas et Rodríguez Peña, *A. Ruiz Leal 3787* (holotype: SI [SI002507]).

Strombocarpa strombulifera* var. *strombulifera

Mimosa retortunium Lam., Encycl. 1: 15. 1783, nom. invalid pro syn.
Mimosa circinalis Cav., Icon. 6: 41. 1801, nom. illeg.
Spirolobium australe A.D. Orb., Voy. Amér. Mér. 8 (Atlas, Bot): t. 13. 1839.

***Strombocarpa tamarugo* (Phil.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303583-1

Basionym. *Prosopis tamarugo* Phil., Anales Mus. Nac. Santiago de Chile 1891: 21. 1891.

Type material. Chile. Prov. Tarapacá, Valle de Tamarugal, *F. Philippi 1840* (holotype: SGO [SGO000002445]; isotype: SI [SI002508]).

***Strombocarpa torquata* (Lag.) Hutch., Gen. Fl. Pl. 1: 287. 1964.**

Acacia torquata Lag., Gen. Sp. Pl.: 16, 206. 1816.
Prosopis torquata (Lag.) DC., Prodr. 2: 448. 1825.
Prosopis adesmioides Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 132. 1874.

Type material. probably t.36, ined., del Hortus de Cavanilles (fide Burkart in Darwiniana 4: 66. 1940).

***Neltuma* Raf., Sylva Tellur.: 119. 1838.**

Prosopis sect. *Algarobia* DC. Prodr. 2: 446. 1825.
Mitostax Raf., Sylva Tellur.: 120. 1838.
Algarobia (DC.) Benth., Pl. Hartw.: 13. 1839.
Prosopis sect. *Monilicarpa* Ruiz Leal ex Burkart, J. Arnold Arbor. 57(3): 230. 1976.

Type. *Neltuma juliflora* (Sw.) Raf. [= *Mimosa juliflora* Sw.].

Description. Spiny, erect to prostrate subshrubs, shrubs and small trees, (0.1–) 4–10 (–20) m high, usually with a short trunk to 40–60 (–>100) cm diameter, branching lax with a spreading rounded or flat-topped crown, twigs cylindrical, flexuous, often arched downwards, glabrous, green or reddish, often with rather long internodes, armed with uninodal axillary, solitary or paired, straight, strong, cylindrical, subulate spines (Figs 2 and 3E), these not necessarily at all nodes, 0.2–15 (–33) cm long × 0.2–1.4 cm in diameter and sometimes thicker than the subtending twig, or with spinescent rigid straight cylindrical branchlets 8–50 cm, brachyblasts congested, blackish. Stipules small, triangular and dry. Leaves with 1–3 (–8) pairs of pinnae, the petiole (0.2–) 2–7.5 cm long, the

pinnular rachises (0.2–) 4–19 (–24.5) cm long, with (1–) 2–30 (–50) pairs of opposite leaflets, these linear, ovate-oblong, oblong-linear or lance-ovate, more or less acute, palmately pinnativeined or almost without veins, (0.15–) 2.5–10 × 0.05–3.5 cm, puberulous to scarcely ciliolate or glabrous, or sometimes aphyllous or subaphyllous (*N. sericantha*, *N. kuntzei*), the leaves small and soon falling off the young developing shoots which become spinescent. Inflorescences axillary, solitary or fascicled, spicate, (1.5–) 3–15 cm long with 20–250 flowers on short 1.6 mm pedicels. Flowers white, yellow, greenish-yellow or occasionally red, often perfumed, sometimes some functionally male flowers; calyx 1–2 mm long; corolla 3–5 mm long, the petals almost free, pubescent, usually villous within; stamens and style exserted, anthers with a minute caducous incurved claviform gland arising from the connective. Fruits linear moniliform or compressed turgid (Figs 6 and 7H–I), straw yellow, sometimes tinged reddish-maroon or black, 1–several per infructescence, indehiscent, glabrous, mostly straight to subfalcate, S- or C-shaped or annular with 1–3 very lax open spirals, acuminate, (2–) 5–29 cm in length × 0.5–2.6 cm diameter, margins often thickened and undulate, valves striate corrugate or smooth, exocarp crustaceous, mesocarp thin or more usually thick and pulpy, mealy or spongy, dry, usually sweet, endocarp hard and bony or coriaceous, with convex faces and acute extremities, segmented in longitudinal or transverse subquadrate closed seed chambers. Seeds brown, compressed ovate, 5–10 × 3–6 mm. See also Johnston (1962).

Geographic distribution. Potentially up to 43 species, but probably somewhat fewer (see below). Widespread across seasonally dry tropical and arid regions of the Americas with a pseudo-amphitropical bicentric pattern of greatest species diversity in the Mexican-Texan and Argentinian-Chilean-Paraguayan regions, especially diverse and abundant in the Chaco, with an outlying disjunct occurrence of *Neltuma ruscifolia* of questionable nativity in the Caatinga in north-east Brazil (Burkart 1976; Oliveira & Queiroz 2020) and extending into warm and some colder temperate areas in Texas and Nevada in the north and Patagonia in the south, where *N. denudans* Benth. reaches 48 °S (Fig. 8).

Habitat and uses. Dominant across large tracts of the Gran Chaco in mixed sub-xerophyllous woodland, also in Monte vegetation, open desert forests in quebradas along seasonal rivers, in *Stipa*-dominated pampas and semi-desert shrub steppe with hot summers and cold winters in Patagonia as far as 48 °S, some species capable of surviving extreme drought; spanning a wide range of substrates and edaphic conditions including stony and sandy mesas, coastal and inland sand dunes and deep black seasonally inundated, sometimes saline, clay vertisols. Some species weedy and invasive, both within their native ranges and where introduced (see Introduction). The wood generally hard, dense, durable and flexible and widely used for fence posts, parquet flooring, barrels, firewood and charcoal and the fruits are eagerly consumed by all forms of livestock (see Introduction).

Etymology. Possibly derived from the common name *Mulla Thumma* in the Dravidian language Teluga in the Indian states of Andhra Pradesh and Telangana, where *Neltuma juliflora* is introduced.

Affinities. *Neltuma* is sister to, but deeply divergent from, the combined *Strombocarpa* + *Xerocladia* clade (Fig. 1).

Thirteen species of *Prosopis* have been described since the publication of Burkart's (1976) monograph. One of these, *Prosopis bonplanda* P.R. Earl & Lux, was already

placed in synonymy under *P. glandulosa* by Palacios (2006). All of the rest can be confidently placed in *Neltuma* (= *Prosopis* sect. *Algarobia* + *Prosopis* sect. *Monilicarpa*), based on morphological descriptions and illustrations from their respective protologues. We provide new combinations in *Neltuma* for all these names, listing potentially up to 43 species for the genus, but we suspect that some of these new species may be no more than regional variants of the widespread and taxonomically difficult *N. pallida* / *N. juliflora* species complex. Given the difficulties of species delimitation across parts of *Neltuma*, we suggest that a detailed molecular study with complete sampling of species and dense sampling of multiple accessions, representing intraspecific diversity, is needed to properly re-assess species boundaries and possible hybridisation. The *Mimobaits* gene set of Koenen et al. (2020) would be an ideal tool for such a study.

***Neltuma affinis* (Spreng.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303584-1

Prosopis algarobilla Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 131. 1874.
Prosopis nandubey Lorentz ex Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 117. 1879.
Prosopis algarobilla var. *nandubay* (Lorentz ex Griseb.) Hassl., Repert. Spec. Nov. Regni Veg. 16: 154. 1919.

Basionym. *Prosopis affinis* Spreng., Syst. Veg. 2: 326. 1825.

Type material. Uruguay. Montevideo, *F. Sello s.n.* (lectotype (designated by Burkart 1976: 491): MO [MO-954306]).

***Neltuma alba* (Griseb.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303585-1

Basionym. *Prosopis alba* Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 131. 1874.

Type material. Argentina. Córdoba, Estancia Germania, *Lorentz 5* (isotypes: F [F0BN001457], M [M0218675], MPU [MPU016115], SI [SI002458]).

Neltuma alba* var. *alba

Prosopis siliquastrum var. *longisiliqua* Phil., Anales Mus. Nac. Santiago de Chile 1: 20. 1891.
Prosopis atacamensis Phil., Anales Univ. Chile 84: 444. 1893.

***Neltuma alba* var. *panta* (Griseb.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303586-1

Prosopis panta (Griseb.) Hieron., Bol. Acad. Nac. Ci. Republ. Argent. 4: 284. 1881.

Basionym. *Prosopis alba* var. *panta* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 118. 1879.

Type material. Argentina. Córdoba, *Lorentz s.n.*

***Neltuma alpataco* (Phil.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303587-1

Basionym. *Prosopis alpataco* Phil., Anales Univ. Chile 21(2): 394. 1862.

Type material. Argentina. nr Mendoza, *W. Diaz s.n.* (probable isotypes: SGO [SGO000002428], SI [SI002464]).

Neltuma alpataco* var. *alpataco

Prosopis stenoloba Phil., Anales Mus. Nac. Santiago de Chile 1: 20. 1891.

***Neltuma alpataco* var. *lamaro* (F.A. Roig) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303588-1

Basionym. *Prosopis alpataco* var. *lamaro* F.A. Roig, Parodiana 5: 56. 1987. (publ. 1988).

Type material. Argentina. *Roig 8946* (holotype: MERL).

***Neltuma alpataco* f. *rubra* (F.A. Roig) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303589-1

Basionym. *Prosopis alpataco* f. *rubra* F.A. Roig, Parodiana 5: 56. 1987. (publ. 1988).

Type material. Argentina. *Roig et al. 223* (holotype: MERL).

***Neltuma andicola* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303590-1

Prosopis andicola (Burkart) A. Galán, E. Linares, J. Montoya & Vicente Orell., Phytotaxa 414: 49. 2019.

Basionym. *Prosopis laevigata* var. *andicola* Burkart, J. Arnold Arbor. 57: 510. 1976.

Type material. Peru. Cuzco, Prov. Calca, Hacienda Urco, *J.C. Vargas-Calderón 709* (holotype: SI [SI002483]).

Neltuma argentina **(Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303591-1

Basionym. *Prosopis argentina* Burkart, Revista Argent. Agron. 4: 39. 1937.

Type material. Argentina. Catamarca: Fiambalá, *A. Castellanos s.n.* (holotype: CTES [CTES0000667]; isotype: SI [SI002606]).

Neltuma articulata **(S. Watson) Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 187. 1928.**

Prosopis articulata S. Watson, Proc. Amer. Acad. Arts 24: 48. 1889.
Prosopis juliflora var. *articulata* (S. Watson) Wiggins, Contr. Dudley Herb. 4: 17. 1950.
Neltuma pazensis Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 187. 1928.
Prosopis pazensis (Britton & Rose) Wiggins, Contr. Dudley Herb. 4: 18. 1950.

Type material. Mexico. Sonora, Guaymas, *E. Palmer 197* (lectotype designated by Palacios (2006): GH [GH00003478]; isolectotypes: BM [BM000952297, BM000952297], K [K000478261], NY [NY00005127], US [US00000983, US00930831], YU [YU001419]).

Neltuma caldenia **(Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303592-1

Prosopis dulcis Gillies ex Hook., Bot. Misc. 3: 203. 1833, nom. illeg.
Prosopis calden Monticelli, Lilloa 3: 348. 1939, nom. nud.

Basionym. *Prosopis caldenia* Burkart, Darwiniana 3: 111. 1939.

Type material. Argentina. San Luis: Sierra, El Volcán (cerca de la capital), *A.L. Pastore s.n., Herb Burkart 6629* (holotype: SI [SI002466]).

Neltuma calderensis **(A. Galán, E. Linares, J. Montoya & Vicente Orell.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303593-1

Basionym. *Prosopis calderensis* A. Galán, E. Linares, J. Montoya & Vicente Orell., Phytotaxa 414: 50. 2019.

Type material. Peru. Arequipa: Mollebaya, *A. Galán et al. AG4633* (holotype: CPUN, isotypes: HUSA, MA, MO, USP).

Neltuma calingastana **(Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303594-1

Basionym. *Prosopis calingastana* Burkart, Bol. Soc. Argent. Bot. 6: 223. 1957.

Type material. Argentina. San Juan, Calingasta, Quebrada Las Leñas y Est. Las Hornillas, Valle de Los Patos, *Moreau & Perrone s.n.* (*BA55032*) (holotype: SI [SI002468]).

Neltuma campestris **(Griseb.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303595-1

Basionym. *Prosopis campestris* Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 132. 1874.

Type material. Argentina. Córdoba, pr. Chañar, *P.G. Lorentz 2* (holotype: GOET [GOET009644]; isotypes: CORD [CORD00005674], F [F0BN001459], SI [SI002469]).

Neltuma castellanosii **(Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303728-1

Basionym. *Prosopis castellanosii* Burkart, Darwiniana 5: 66. 1941.

Type material. Argentina. Mendoza: Payún-Matrú, *A. Castellanos 14253* (*BA 36732*) (holotype: SI [SI002471]; isotypes: LIL [LIL000715], GH [GH00063863]).

Neltuma chilensis **(Molina) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303729-1

Prosopis chilensis (Molina) Stuntz, U.S.D.A. Bur. Pl. Industr. Invent. Seeds 31: 85. 1914.

Basionym. *Ceratonia chilensis* Molina, Sag. Stor. Nat. Chili: 172. 1782.

Type material. Chile. (no type details given in protologue to *Ceratonia chilensis*).

Neltuma chilensis **var.** ***catamarcana*** **(Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303730-1

Basionym. *Prosopis chilensis* var. *catamarcana* Burkart, J. Arnold Arbor. 57: 497. 1976.

Type material. Argentina. Prov. Catamarca, Dept. Belén, *Ulibarri 581* (holotype: SI [SI002472, SI002473]).

Neltuma chilensis **var.** ***chilensis***

Acacia siliquastrum Cav. ex Lag., Gen. Sp. Pl.: 16. 1816.

Prosopis siliquastrum (Cav. ex Lag.) DC., Prodr. 2: 447. 1825.
Prosopis siliquosa St.-Lag., Ann. Soc. Bot. Lyon 7: 132. 1880, orth. var.
Prosopis schinopoma Stuck., Bull. Acad. Int. Géogr. Bot. 13: 87. 1904.

***Neltuma chilensis* var. *riojana* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303731-1

Basionym. *Prosopis chilensis* var. *riojana* Burkart, Darwiniana 9: 75. 1949.

Type material. Argentina. Prov. de La Rioja: Quebrada de lka Troya, cerca de Jagüel, *A. Burkart 12355* (holotype: SI [SI002474]).

***Neltuma denudans* (Benth.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303732-1

Basionym. *Prosopis denudans* Benth., J. Bot. (Hooker) 4: 351. 1842.

Type material. Argentina. Patagonia, Santa Cruz, near Puerto Deseado ("Port Desire"), *Middleton s.n.* (holotype: K [K000504789]).

Neltuma denudans* var. *denudans

***Neltuma denudans* var. *patagonica* (Speg.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303733-1

Prosopis denudans var. *patagonica* (Speg.) Burkart, J. Arnold Arbor. 57: 480. 1976.

Basionym. *Prosopis patagonica* Speg., Revista Fac. Agron. Univ. Nac. La Plata 3: 510. 1897.

Type material. Argentina. Patagonia, "Golfo de San Jorge ", *C. Spegazzini s.n.*

***Neltuma denudans* var. *stenocarpa* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303734-1

Basionym. *Prosopis denudans* var. *stenocarpa* Burkart, Darwiniana 9: 75. 1949.

Type material. Argentina. Gob. del Chubut: Dept. Rawson, south of Trelew, *A. Krapovickas 4367* (isotypes: SI [SI002475, SI002476], BAB [BAB00000476]).

***Neltuma elata* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303735-1

Prosopis elata (Burkart) Burkart, Legum. Argent., ed. 2: 544. 1952.

Basionym. *Prosopis campestris* var. *elata* Burkart, Darwiniana 4: 112. 1940.

Type material. Paraguay. Chaco, Puesto Buenos Aires, en el sector Pilcomayo, *T. Rojas 8323* (holotype: SI [SI002477]).

***Neltuma fiebrigii* (Harms) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303736-1

Basionym. *Prosopis fiebrigii* Harms, Repert. Spec. Nov. Regni Veg. 13: 524. 1915.

Type material. Paraguay. Chaco, *Fiebrig 1254* (isotypes: F [F0BN001462, F0058760F, F0360901F], G [G00400139], K [K000504802], M [M0218669]).

***Neltuma flexuosa* (DC.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303737-1

Acacia flexuosa Lag., Gen. Sp. Pl.: 16 (1816), nom. illeg.

Basionym. *Prosopis flexuosa* DC., Prodr. 2: 447. 1825.

Type material. Chile.

***Neltuma flexuosa* var. *depressa* (F.A. Roig) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303738-1

Prosopis juliflora f. *fruticosa* Hauman, Anales Mus. Nac. Hist. Nat. Buenos Aires 24: 391. 1913.
Prosopis alba f. *fruticosa* (Hauman) Monticelli, Lilloa 3: 347. 1938.

Basionym. *Prosopis flexuosa* var. *depressa* F.A. Roig, Parodiana 5: 53. 1987 (publ. 1988).

Type material. Argentina. Mendoza, Depto. Malargüe, Matancilla, *Roig et al. "coleción Sierra de Chachahuén 32"* (neotype: MERL).

Neltuma flexuosa* var. *flexuosa

Prosopis juliflora f. *arborea* Hauman, Anales Mus. Nac. Hist. Nat. Buenos Aires 24: 391. 1913.

***Neltuma flexuosa* var. *fruticosa* (Meyen) C.E. Hughes & G.P. Lewis**

Prosopis flexuosa var. *fruticosa* (Meyen) F.A. Roig, Parodiana 5: 53. 1987. (publ. 1988).

Basionym. *Prosopis fruticosa* Meyen, Observ. Bot. 1: 376. 1834.
Type material. Chile. Prov. de Copiapó, *Roig 12536* (holotype: MERL).

***Neltuma flexuosa* f. *subinermis* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303739-1

Basionym. *Prosopis flexuosa* f. *subinermis* Burkart, J. Arnold Arbor. 57: 513. 1976.
Type material. Argentina. San Juan: Calingasta a Barreal, entre La Isla y Sorocayense, *J.H. Hunziker 6451* (holotype: SI).

***Neltuma glandulosa* (Torr.) Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 186 (1928).**

Prosopis glandulosa Torr., Ann. Lyceum Nat. Hist. New York 2: 192. 1827.
Dasiogyna glandulosa (Torr.) Raf., Atlantic J. 1: 146. 1832.
Algarobia glandulosa (Torr.) Torr. & A. Gray, Fl. N. Amer. 1: 399. 1840.
Prosopis juliflora var. *glandulosa* (Torr.) Cockerell, Bull. New Mexico Agric. Exp. Sta. 15: 58. 1895.
Prosopis chilensis var. *glandulosa* (Torr.) Standl., Contr. U.S. Natl. Herb. 23: 1658. 1926.

Type material. U.S.A. New Mexico, Union County, Major Long`s Creek (a tributary of the Canadian River ("on the Canadian"), *James s.n.* (holotype: NY [NY00005945]).

Neltuma glandulosa* var. *glandulosa

Prosopis juliflora var. *constricta* Sarg., Trees & Shrubs 2: 249. 1913.
Neltuma constricta (Sarg.) Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 186. 1928.
Neltuma neomexicana Britton, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 186. 1928.
Prosopis bonplanda P.R. Earl & Lux. Publ. Biol. FCB/UANL. Mex. 5 (2): 38. 1991.

***Neltuma glandulosa* var. *prostrata* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303740-1

Basionym. *Prosopis glandulosa* var. *prostrata* Burkart, J. Arnold Arbor. 57: 516. 1976.
Type material. U.S.A. Texas: Kleberg County, western part of Laureles Division of King Ranch, *M.C. Johnston 54359* (holotype: COLO; isotype SI [SI015053]).

***Neltuma hassleri* (Harms) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303741-1

Basionym. *Prosopis hassleri* Harms, Repert. Spec. Nov. Regni Veg.13: 523. 1915.

Type material. Paraguay. river Pilcomayo, Puerto Tolderia, *T. Rojas 329* (isotypes: A [A00063864], BM [BM000545192], F [F0BN001463, F0360902F], GH, P).

Neltuma hassleri* var. *hassleri

***Neltuma hassleri* var. *nigroides* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303742-1

Basionym. *Prosopis hassleri* var. *nigroides* Burkart, J. Arnold Arbor. 57: 479. 1976.

Type material. Argentina. Prov. Santa Fe: Dept. General Obligado, Estancia Las Camelias, *A.E. Ragonese 2423* (holotype: SI [SI002481]).

***Neltuma humilis* (Gillies ex Hook.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303743-1

Basionym. *Prosopis humilis* Gillies ex Hook., Bot. Misc. 3: 204. 1833.

Type material. Argentina. in the Pampas of Buenos Aires ("Ayres"), *J. Gilles s.n.* (holotype: K [K000504787]; isotypes: E [E00158975, E00158976]).

***Neltuma juliflora* (Sw.) Raf., Sylva Tellur.: 119. 1838.**

Mimosa juliflora Sw., Prodr. Veg. Ind. Occ.: 85. 1788.
Acacia juliflora (Sw.) Willd., Sp. Pl., ed. 4, 4: 1076. 1806.
Prosopis juliflora (Sw.) DC., Prodr. 2: 447. 1825.
Algarobia juliflora (Sw.) Heynh., Alph. Aufz. Gew.: 18. 1846.
Entada juliflora (Sw.) Roberty, Bull. Inst. Fondam. Afrique Noire, Sér. A, Sci. Nat. 16: 346. 1954.

Type material. Jamaica. *O.P. Swartz s.n.* (S [S-R-3632, S06-5737]).

***Neltuma juliflora* var. *horrida* (Kunth) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303744-1

Prosopis juliflora var. *horrida* (Kunth) Burkart, J. Arnold Arbor. 57: 502. 1976.

Basionym. *Prosopis horrida* Kunth, Mimoses: 106. 1822.

Type material. Peru. "crescit ad radices Andium orientalium, juxta ripam fluminis Amazonum, inter Tomependa(m) et confluentem Chamaya; item prope litus Oceani Pacifici, in arenosis, inter Piura(m) et Lambayeque", *Humboldt & Bonpland 3603* (isotypes: P [P00679172, P02734496]).

Neltuma juliflora* var. *juliflora

Mimosa piliflora Sw., Fl. Ind. Occid. 2: 986. 1800.
Mimosa furcata Desf., Tabl. École Bot.: 180. 1804.
Acacia cumanensis Humb. & Bonpl. ex Willd., Sp. Pl., ed. 4, 4: 1058. 1806.
Mimosa salinarum Vahl, Eclog. Amer. 3: 35. 1807.
Acacia diptera Humb. & Bonpl. ex Willd., Enum. Pl.: 1051. 1809.
Mimosa algarrobo Azara, Voy. Amér. Mér. 2: 483. 1809.
Mimosa cumana Poir., in J.B.A.M. de Lamarck, Encycl., Suppl. 1: 65. 1810.
Mimosa levigata Poir., in J.B.A.M. de Lamarck, Encycl., Suppl. 1: 65. 1810.
Mimosa pallida Poir., in J.B.A.M. de Lamarck, Encycl., Suppl. 1: 65. 1810.
Acacia furcata (Desf.) Desv., J. Bot. Agric. 3: 67. 1814.
Acacia falcata Desf., Tabl. École Bot., ed. 2: 207. 1815, nom. illeg.
Mimosa diptera Poir., in J.B.A.M. de Lamarck, Encycl., Suppl. 5: 529. 1817.
Desmanthus salinarum (Vahl) Steud., Nomencl. Bot. 1: 269. 1821.
Prosopis cumanensis Kunth, in F.W.H. von Humboldt, A.J.A. Bonpland & C.S. Kunth, Nov. Gen. Sp. 6: 310. 1824.
Prosopis inermis Kunth, in F.W.H. von Humboldt, A.J.A. Bonpland & C.S. Kunth, Nov. Gen. Sp. 6: 307. 1824.
Acacia salinarum (Vahl) DC., Prodr. 2: 456. 1825.
Prosopis bracteolata DC., Prodr. 2: 447. 1825.
Prosopis domingensis DC., Prodr. 2: 447. 1825.
Mimosa pseudoschinus Terán & Berland., Mem. Comis. Limites: 11. 1832.
Algarobia dulcis Benth., Pl. Hartw.: 13. 1839.
Prosopis dulcis var. *domingensis* (DC.) Benth., J. Bot. (Hooker) 4: 350. 1842.
Mimosa laevigata Benth., Linnaea 22: 530. 1849, orth. var.
Prosopis vidaliana Náves, Descr. *Prosopsis vidaliana*: 15. 1877.
Neltuma bakeri Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 185. 1928.
Neltuma occidentalis Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 185. 1928.
Neltuma pallescens Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 185. 1928.
Prosopis juliflora var. *inermis* (Kunth) Burkart, J. Arnold Arbor. 57: 502. 1976.

***Neltuma kuntzei* (Harms ex C.E.O. Kuntze) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303745-1

Prosopis barba-tigridis Stuck., Comun. Mus. Nac. Buenos Aires 1: 66. 1899.
Prosopis casadensis Penz., Malpighia 12: 408. 1899.

Basionym. *Prosopis kuntzei* Harms ex C.E.O. Kuntze, Revis. Gen. Pl. 3(2): 71. 1898.

Type material. Bolivia. Sierra de Santa Cruz, *O. Kuntze s.n.* (isotypes: F [F0BN001465], NY [NY00003276], US [US00000986]).

***Neltuma laevigata* (Humb. & Bonpl. ex Willd.) Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 187. 1928.**

Acacia laevigata Humb. & Bonpl. ex Willd., Sp. Pl., ed. 4, 4: 1059. 1806.
Prosopis laevigata (Humb. & Bonpl. ex Willd.) M.C. Johnst., Brittonia 14: 78. 1962.
Prosopis dulcis Kunth, Mimoses: 110. 1822.
Acacia tortuosa Billb. ex Beurl., Kongl. Svenska Vetensk. Acad. Handl., n.s., 2: 24. 1856, nom. illeg.
Mimosa rotundata Sessé & Moc., Pl. Nov. Hisp.: 178. 1890.
Neltuma michoacana Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 187. 1928.

Type material. Mexico. "in America meridionali", Morelos, between Huajintlán ("Guasintlan ") and Puente de Istla, fide Johnston (1962), *Humboldt & Bonpland* (holotype B, microfiche reproduction Herbarium Willdenow Cat. N. 19132 (MO), fide Palacios (2006).

***Neltuma limensis* (Benth.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303746-1

Basionym. *Prosopis limensis* Benth., J. Bot. (Hooker) 4: 350. 1842.

Type material. Peru. Lima, *H. Cuming 974* (lectotype designated by Perry 1998. Fl. Australia 12: 193; isolectotypes: BM [BM000952294], E [E00319916, E00319926], GH [GH00063865], K [K000821140], US).

***Neltuma mantaroensis* (L. Vásquez, Escurra & Huamán) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303747-1

Basionym. *Prosopis mantaroensis* L. Vásquez, Escurra & Huamán, Sciéndo 12(1): 70. 2009.

Type material. Peru. Ayacucho, Prov. Huanta, Distr. Huanta, *L. Vásquez Núñez et al. 12845* (holotype: PRG; isotype: PRG).

***Neltuma mayana* (R.A. Palacios) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303748-1

Basionym. *Prosopis mayana* R.A. Palacios, Bol. Soc. Argent. Bot. 41: 115. 2006.

Type material. Mexico. Yucatán, entre Dzilam de Bravo y El Tajo, *R. Palacios 2362* (holotype: MEXU [MEXU01241933]; isotypes: BAFC, TEX [TEX00202236]).

***Neltuma mezcalana* (R.A. Palacios) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303749-1

Basionym. *Prosopis mezcalana* R.A. Palacios, Bol. Soc. Argent. Bot. 41: 105. 2006.

Type material. Mexico. Guerrero, entrada a Chacamerito y Tanganhuato, *R. Palacios 2402* (holotype: MEXU; isotypes: BAFC, TEX [TEX00202211]).

***Neltuma nigra* (Griseb.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303750-1

Prosopis nigra (Griseb.) Hieron., Bol. Acad. Nac. Ci. Republ. Argent. 4: 283. 1881.

Basionym. *Prosopis algarobilla* var. *nigra* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 118. 1879.

Type material. Argentina. Córdoba, prope urban Chacra de la Merced, *C. Galander s.n.* (?holotype: HBG [HBG519250].

***Neltuma nigra* var. *longispina* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303751-1

Basionym. *Prosopis nigra* var. *longispina* Burkart, J. Arnold Arbor. 57: 507. 1976.

Type material. Argentina. Prov. Corrientes, Dept. Capital, 2 km S of Paso Pessoa, *T.M. Pedersen 2808* (holotype: SI [SI002485]; isotypes: C [C10012323], CTES [CTES0000668], L [L0019214], MO [MO-954304], WAG [WAG0132133]).

Neltuma nigra* var. *nigra

Prosopis dulcis var. *australis* Benth., J. Bot. (Hooker) 4: 350. 1842.

***Neltuma nigra* var. *ragonesei* (Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303752-1

Basionym. *Prosopis nigra* var. *ragonesei* Burkart, Darwiniana 7: 518. 1947.

Type material. Argentina. Santa Fe: Videla, *A.E. Ragonese 2078* (holotype: SI [SI002490]).

***Neltuma nuda* (Schinini) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303753-1

Basionym. *Prosopis nuda* Schinini, Bonplandia (Corrientes) 5: 105. 1981.

Type material. Paraguay. Dep. Boquerón. Mariscal Estigarribia, *A. Schinini* & *E.E. Bordas 15222* (holotype: CTES [CTES0000670]; isotype: SI [SI002493]).

***Neltuma odorata* (Torr. & Frém.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303754-1

Strombocarpa odorata (Torr. & Frém.) A. Gray, U.S. Expl. Exped., Phan. 1: 475. 1854.
Prosopis juliflora var. *torreyana* L.D. Benson, Amer. J. Bot. 28: 751. 1941.
Prosopis glandulosa var. *torreyana* (L.D. Benson) M.C. Johnst., Brittonia 14: 82. 1962.
Prosopis glandulosa subsp. *torreyana* (L.D. Benson) A.E. Murray, Kalmia 12: 23. 1982.

Basionym. *Prosopis odorata* Torr. & Frém., in J.C. Frémont, Rep. Exped. Rocky Mts.: 313. Pl. 1. 1845. Pro parte, excluding the fruits, fide L. D. Benson Madroño 15: 53. 1959.

Type material. U.S.A. California, along Mohave and Virgin River, *Fremont s.n.* (lectotype designated Benson (1959): NY), excluding the fruits.

***Neltuma pallida* (Humb. & Bonpl. ex Willd.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303755-1

Prosopis pallida (Humb. & Bonpl. ex Willd.) Kunth, in F.W.H. von Humboldt, A.J.A. Bonpland & C.S. Kunth, Nov. Gen. Sp. 6: 309. 1824.
Mitostax pallida (Humb. & Bonpl. ex Willd.) Raf., Sylva Tellur.: 120. 1838.

Basionym. *Acacia pallida* Humb. & Bonpl. ex Willd., Sp. Pl., ed. 4, 4: 1059. 1806.

Type material. Peru. Prov. Jaén de Bracamoros, Passo de Matara, "in America meridionali", ?Bonpland.

Neltuma palmeri **Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 185. 1928.**

Prosopis tamaulipana Burkart, J. Arnold Arbor. 57: 494. 1976.

Type material. Mexico. Tamaulipas: vicinity of Victoria, *E. Palmer 400* (holotype: NY [NY00005077]; isotypes: CM [CM1060], GH, MO [MO-356247], US [US00000993]).

Although the nom. nov. *P. tamaulipana* Burkart was required when *Neltuma palmeri* Britton & Rose was transferred to *Prosopis* because the name *Prosopis palmeri* S. Watson (= *Strombocarpa palmeri* (S.Watson) C.E. Hughes & G.P. Lewis) was already occupied, the original *N. palmeri* provides a valid accepted name.

Neltuma peruviana **(L. Vásquez, Escurra & Huamán) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303756-1

Basionym. *Prosopis peruviana* L. Vásquez, Escurra & Huamán, Sciéndo 12(1): 74. 2009.

Type material. Peru. Apurímac, Prov. Andahuaylas, Distr. Sapichaca, *L. Vásquez Núñez et al. 12849* (holotype: PRG; isotype: PRG).

Neltuma piurensis **(L. Vásquez, Escurra & Huamán) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303757-1

Basionym. *Prosopis piurensis* L. Vásquez, Escurra & Huamán, Sciéndo 12(1): 76. 2009.

Type material. Peru. Piura, Prov. Sullana, borde de carretera panamericana cerca al Puente del rio Chira, *L. Vásquez Núñez et al. 13258* (holotype: PRG).

Neltuma pugionata **(Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303758-1

Basionym. *Prosopis pugionata* Burkart, Darwiniana 9: 70. 1949.

Type material. Argentina. Prov. de Córdoba, extremo noroeste, bosques xerófilos a las Salinas Grandes, km 907, *A.E. Ragonese & B. Piccinini 6097* (holotype: BAB [BAB00000478]; isotype: SI [SI002497]).

Neltuma purpurea **(L. Vásquez, Escurra & Huamán) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303759-1

Basionym. *Prosopis purpurea* L. Vásquez, Escurra & Huamán, Sciéndo 12(1): 79. 2009.

Type material. Peru. Tumbes, Distr. Puerto Pizarro, *L. Vásquez Núñez et al. 12941* (holotype: PRG; isotype: PRG).

Neltuma rojasiana **(Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303760-1

Basionym. *Prosopis rojasiana* Burkart, Darwiniana 5: 70. 1941.

Type material. Paraguay. Chaco paraguayo, Sector López de Filippis, *Rojas 8310* (holotype: SI [SI002500]).

Neltuma rubriflora **(Hassl.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303761-1

Basionym. *Prosopis rubriflora* Hassl., Repert. Spec. Nov. Regni Veg. 8: 552. 1910.

Type material. Paraguay. Centurión, zwischen Apa und Aquidaban, *K. Fiebrig 5348* (isotypes: F [F0BN001468], GH [GH00063869], HBG [HBG519244], M [M0218666], P [P02436145], fragment SI [SI002502]).

Neltuma ruizlealii **(Burkart) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303762-1

Basionym. *Prosopis ruizlealii* Burkart, Darwiniana 4: 328. 1942.

Type material. Argentina. Prov. Mendoza, Dep. San Rafael: Agua del Sapo, *Ruiz Leal 7358* (holotype: SI).

Neltuma ruscifolia **(Griseb.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303763-1

Basionym. *Prosopis ruscifolia* Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 130. 1874.

Type material. Argentina. Santiago del Estero, *P.G. Lorentz 21* (holotype: GOET [GOET009549]; isotypes: CORD [CORD00005670], SI [SI002504]).

Neltuma sericantha **(Gillies ex Hook.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303764-1

Basionym. *Prosopis sericantha* Gillies ex Hook., Bot. Misc. 3: 204. 1833.
Type material. Argentina. Prov. San Luis, *J. Gilles s.n.* (holotype: K [K000504780]; isotypes: E [E00180081, E00180082], GH [GH00063870]).

Neltuma tupayachensis **(L. Vásquez, Escurra & Huamán) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303765-1

Basionym. *Prosopis tupayachensis* L. Vásquez, Escurra & Huamán, Sciéndo 12(1): 82. 2009.
Type material. Peru. Prov. Cuzco, Distr. Lucre, *L. Vásquez Núñez et al. 12846* (holotype: PRG; isotype: PRG).

Neltuma velutina **(Wooton) Britton & Rose, in N.L. Britton & al. (eds.), N. Amer. Fl. 23: 186. 1928.**

Prosopis velutina Wooton, Bull. Torrey Bot. Club 25: 456. 1898.
Prosopis juliflora var. *velutina* (Wooton) Sarg., Silva N. Amer. 13: 15. 1902.
Prosopis chilensis var. *velutina* (Wooton) Standl., Contr. U.S. Natl. Herb. 23: 1658. 1926.

Type material. U.S.A. Arizona, without further locality, *Pringle 13665* (lectotype NY [NY00003272] designated by Britton & Rose in N. Am. Fl. 23(3): 186. 1928; isolectotypes: A [A00003470], CM [CM1091], MO [MO-954307]).

Neltuma **×** ***vinalillo*** **(Stuck.) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303766-1

N. alba var. *panta* (as *P. panta*)× *N. ruscifolia*.

Basionym. *Prosopis* × *vinalillo* Stuck., Anales Mus. Nac. Buenos Aires 7 (ser. 2, t. 4): 73. 1902.
Type material. Argentina. Prov. Tucumán: Depto. De Burruyaco, ? Cañada Alegre.

Neltuma yaquiana **(R.A. Palacios) C.E. Hughes & G.P. Lewis, comb. nov.**
urn:lsid:ipni.org:names:77303767-1

Basionym. *Prosopis yaquiana* R.A. Palacios, Bol. Soc. Argent. Bot. 41: 117. 2006.

Type material. Mexico. Sinaloa, alrededores del Cementerio de Topolobampo, *R. Palacios 2417* (holotype: MEXU; isotypes: BAFC, TEX [TEX00202225]).

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